SURVIVAL OF DUCK NESTS, DISTRIBUTION OF DUCK BROODS, AND HABITAT CONSERVATION TARGETING IN THE PRAIRIE POTHOLE REGION

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Abstract

The Prairie Pothole Region (PPR) is an important breeding region for populations of upland-nesting ducks (*Anas* spp.). I studied survival of duck nests, distribution of duck broods, and conservation easement targeting in the PPR of North and South Dakota, USA. Nest survival of common duck species varied from 0.02 ($\widehat{SE}$ = 0.01) to 0.23 ($\widehat{SE}$ = 0.02) among study sites and years and was positively related to current pond density and primary productivity and negatively related to recent pond density and primary productivity. This result was consistent with the hypothesis that nest predators and thus nest survival were responding to changes in productivity induced by relatively short-term (1yr-2yr) precipitation cycles. Distribution of broods was positively related to wetland area and proportion of perennial grass cover on the study site. Estimated probability of wetland occupancy for a brood of a representative species, gadwall (*Anas strepera*), increased from 0.08 (90% Credible Interval: 0.07, 0.10) to 0.28 (0.24, 0.33) as wetland area increased from 0.19 ha to 2.12 ha. As proportion of perennial grass cover on a study site increased from 0.03 to 0.99, estimated probability of wetland occupancy by a gadwall brood increased from 0.12 (0.09, 0.16) to 0.20 (0.16, 0.25). These relationships identified wetland basins and landscapes with a higher probability of occupancy. The extensive repeat-visit brood survey was therefore a useful way to learn about the distribution of duck broods across a large geographic extent. I also investigated need and opportunity to refine current habitat protection strategies in the PPR. Area of habitat protected declined annually during 2000–2009 while cost of protection increased 248% from $210/ha to $730/ha and cropland rental rates increased 40%. Estimated area protected in 2009 was

210 km^2 (95% Confidence Interval: 133 km^2 to 287 km^2), and 2,792 km^2 was protected during 2000–2009. Refocusing easement acquisition efforts on the 3,189 km^2 that was located in landscapes of highest priority based on pair density and was at relatively high risk of conversion, but was below the 25th percentile of cost provided a 24% reduction in per/hectare cost of protection and a 20% increase in area protected.

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PREFACE

My dissertation comprises three manuscripts prepared for submission to peer-reviewed, professional journals. The first two papers report the results of field investigations of survival of duck nests and the distribution of duck broods in the US Prairie Pothole Region. The third paper provides a critical assessment of current waterfowl habitat conservation activity in the region. I was responsible for all analysis and interpretation, thus I take responsibility for all errors. The "we" contained in the manuscripts refers to myself, my coauthors, and the field personnel who assisted with data collection.

This project resulted from the combined efforts of many organizations and individuals. Ducks Unlimited, Inc., The Prairie Pothole Joint Venture, The North Dakota Game and Fish Department (NDGF), and The South Dakota Department of Game, Fish, and Parks (SDGFP) provided funding. The United States Fish and Wildlife Service, The United States Geological Survey, NDGF, SDGFP, and The Delta Waterfowl Foundation provided in-kind support and assistance with data collection. I appreciate greatly the efforts of numerous, hardworking field assistants who spent many hours gathering data.

I am lucky to have had excellent academic and professional mentors. In particular, I thank my advisory committee: Christine Hunter, Mark Lindberg, Jim Ringelman, and Jay Rotella, for their wise and generous guidance. Many thanks also to Josh Schmidt, Aaron Smith, and Scott Stephens for all of their help and ideas.

Finally, I am grateful to my family, especially Amy and Caity, for their love, support, and patience.

GENERAL INTRODUCTION

My research comprised three studies that focused on the ecology and conservation of breeding dabbling ducks (*Anas* spp.) in the Prairie Pothole Region (PPR) of North and South Dakota. The first study was an investigation of spatial and temporal variation in nest survival probability. The nest survival study was designed to allow rigorous investigation of ecological hypotheses and to result in a deeper understanding of the nesting ecology of ducks and the variable environment of the PPR. The second study was an extensive, repeat-count survey of late-summer brood distribution relative to habitat characteristics. The brood survey used in this study was conceived as a pilot effort for a possible longer-term operational brood survey and monitoring program. This study aimed to evaluate the feasibility and utility of repeat-count brood surveys and hierarchical statistical models for identifying valuable wetland basins and landscapes while correcting for non-detection of broods thus resolving some long-standing issues associated with surveys of unmarked duck broods. The third study was a critical evaluation of a widely used strategy for protecting breeding habitat for ducks through the use of perpetual easements. Specifically, I evaluated whether the addition of information about risk of habitat loss and the cost of protecting habitat would improve the current targeting strategy, which is based only on breeding duck density. The primary objective of this study was to evaluate whether there was a need to change easement targeting strategy given recent increases in the cost of protection.

My first chapter was focused on variation in survival probability of duck nests relative to variation in environmental conditions. In ecosystems where complex spatial

and temporal variation in environmental conditions is evident, we generally have a limited understanding of the impacts of this variability, on populations and thus there are great opportunities for learning (Bissonette and Storch 2007, Gunderson et al. 2007). Relatively few ecological studies have the necessary scope, however, to capture simultaneously an informative cross-section of environmental variation in both space and time (Lindenmayer and Likens 2010). I conducted a multi-site, multi-year, relatively large-scale study of an influential demographic rate of a representative group of duck species in a highly variable environment. This study design allowed me to assess the support for predictions about variation in nest survival relative to variation in environmental conditions at multiple spatial and temporal scales.

Nest survival probability is important to population dynamics of ducks and is strongly influenced by variation in predation rates (Pieron and Rohwer 2010), which in turn are correlated with environmental conditions (Sargeant et al. 1993). Environmental conditions in the PPR are highly variable at spatial scales ranging from several meters to hundreds of kilometers and at temporal scales from ranging from weeks to centuries (Johnson et al. 1994, Shapley et al. 2005). Variation in environmental conditions in the PPR primarily results from variation in wetland communities, land-use practices, and precipitation (Johnson et al. 1994, Millett et al. 2009). Duck populations in the PPR are well-studied, and there is a substantial body of past work on population ecology and demographics of these species which allows construction of hypotheses about variation in nest survival probability relative to environmental conditions. Many past studies of nest survival have focused on either 1) relationships between nest survival probability and

nest-, field-, and landscape-scale spatial variation in vegetation characteristics and land-use practices (e.g., Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005) or 2) relatively unstructured assessments of either spatial or temporal variation in nest survival probability (e.g., Klett et al. 1988, Higgins et al. 1992). Fewer studies have been able to 1) amass a sample of nest survival data that encompass multiple sites and multiple years and 2) relate nest survival probability to both spatial variation in habitat and land-use as well as to spatial and temporal variation in baseline ecosystem drivers like precipitation and primary productivity (Drever et al. 2004).

Drawing on prior knowledge and combining it with new, remotely sensed measurements of environmental conditions, I investigated hypotheses about the responses of nest survival probability to wetland conditions and primary productivity. I also investigated whether nest survival probability was related to both current and recent wetland conditions and primary productivity in a way that was consistent with the hypothesis that pulses of resources are transmitted through the PPR ecosystem at relatively short time scales of 1-2 years. I hypothesized that pulses of precipitation and primary productivity following relatively dry periods might create environmental conditions that result in higher prey availability for nest predators that would result in higher nest survival probability in wet, productive years preceded by dry, unproductive years. The effects of resource pulses are well-known in many ecosystems (e.g., Bissonette and Storch 2007, Thibault et al. 2010), but they have been little studied in the precipitation-driven, wetland-rich environment of the PPR. Resource pulses can create indirect, community-level responses (Meserve et al. 2003) and influence predator-prey

systems in complex ways (Holt 2008, Schmidt and Ostfeld 2008). The nest survival study in Chapter 1 was thus, in large part, an effort to learn more about spatial and temporal variation in nest survival probability and to evaluate the evidence for indirect influences of resource-pulses on duck productivity in the PPR.

For the second chapter of my dissertation, I conducted a study of the relationships between occupancy of wetlands by duck broods and habitat characteristics using an extensive, repeat-visit, survey design and hierarchical statistical models. The PPR is a large region (~700,000 km^2) and upland-nesting ducks are highly mobile animals that disperse widely in response to environmental variation (Lokemoen et al. 1990). Reproductive success is important to population dynamics in these species and is affected by environmental variation at broad spatial and temporal scales (Hoekman et al. 2002). As a result, there has long been great interest in developing a rigorous understanding of spatial and temporal patterns in the distribution and abundance of broods of young ducks late in the breeding season at a regional scale.

Methodologies have been developed for wetland-based brood surveys, but for the most part they rely on individually marked broods or make strict assumptions about detection probability (Ringelman and Flake 1980, Rumble and Flake 1982, Pagano and Arnold 2009). These limitations restrict the application of these methods at broad spatial scales. Recent developments in sampling and analysis methods for presence-absence surveys provided an intriguing alternative that seemed flexible enough to overcome some of the limitations of existing methods (MacKenzie et al. 2006, Royle and Dorazio 2008). Broods are well-suited to presence-absence sampling because they occupy discrete

wetland basins, which can be individually identified. Occupancy of a wetland by a brood provides evidence of wetland use, successful nesting within the local landscape, and survival of ducklings and breeding females to the brood-rearing stage. Regional-scale surveys of brood distribution, as indicated by wetland occupancy, can thus provide a snapshot of landscape-level patterns in reproductive success and habitat use. When conducted over multiple years, these surveys can reveal consistencies in brood distribution and habitat use that would be useful to managers. This potential utility provided a convincing rationale for conducting a large-scale brood survey, and, in 2007, a large group of partners from government agencies, non-governmental conservation organizations, and academic institutions undertook a three-year study of the distribution of duck broods in the PPR with the objective of determining whether a large scale repeat-visit brood survey could provide useful information about the distribution of broods relative to habitat characteristics.

Chapter 2 is based on my analysis of the data from our regional-scale, cooperative brood survey conducted during 2007-2009. This survey provided information about brood occupancy from repeated-visits to a large sample of wetland basins in the PPR. I analyzed these data using hierarchical occupancy models that facilitated simultaneous estimation of probability of occupancy and probability of detection relative to covariates and random-effects (MacKenzie et al. 2006, Royle and Dorazio 2008). This sampling-analytical approach allowed rigorous investigation of a set of ecological predictions about variation in the distribution of broods relative to landscape characteristics and wetland conditions while correcting for variation in detection probability. Our group was

particularly interested in learning whether variation in occupancy was related to land-use and wetland conditions in ways that were consistent with past investigations of other population parameters like density of breeding pairs and nest survival probability.

Although the first two studies in my dissertation had clear connections to management and conservation, they provided no direct comparison to the outcomes or cost of current management practices. Making the transition from research to informed habitat conservation efforts is critical given ongoing loss and degradation of habitat, increasing costs of conservation and protection, and limited budgets for conservation (Pressey et al. 2007). I was therefore very interested in understanding how science has been or could be integrated in recent habitat conservation strategies for breeding waterfowl in the PPR.

A major, and perennial, threat to the future of migratory bird populations in the PPR is conversion of wetland and grassland habitat to annually cultivated cropland (Samson and Knopf 1996, Brennan and Kuvlesky 2005, Hoekstra et al. 2005, Laurance 2010). Limited resources are available to counter this threat and using these resources effectively and efficiently requires a well-informed habitat conservation strategy. In Chapter 3, I evaluated the current strategy for acquisition of perpetual conservation easements in the PPR. Conservation easements are a critical component of the regional conservation strategy for migratory birds, and recent trends in loss rates of habitat, and increases in land prices suggested the capacity for protection might have declined. This created a concern and revealed a potential opportunity to refine the existing strategy. The existing strategy has been based entirely on ranking alternative sites by their expected

density of breeding duck pairs. This benefit-based approach is appealing because of its straightforward rationale, but is widely-known to be inefficient in many systems (Newburn et al. 2005, Naidoo et al. 2006). Conservation strategies that integrate information about the risk of habitat loss and the cost of protecting habitat are often more effective and efficient than solely benefit-based strategies (Newburn et al. 2005). I assessed the need for a more refined targeted strategy in the PPR by estimating recent trends in annual protection and cost, and comparing them to recent land values and projected loss rates. I assessed the value of a more refined targeted strategy by comparing the efficiency of the current strategy to an alternative strategy that combined information on conversion risk, cost of protection, and breeding duck density.

The studies that compose my dissertation develop new perspectives on population ecology, wildlife management, and habitat conservation. The nest survival study (Chapter 1) was one of the most spatially and temporally extensive efforts to study this parameter for any ground-nesting bird species. The brood survey study (Chapter 2) was one of the first and largest efforts to relate the occupancy of wetlands by broods in late-summer to habitat characteristics while correcting for non-detection. The evaluation of easement acquisition and targeting (Chapter 3) was the first attempt to assess the potential efficiency gains associated with incorporating information about risk of habitat loss and cost of protection into habitat conservation targeting in the PPR. Taken as a whole, these studies represent my effort to integrate basic ecology, wildlife management, and conservation planning in a useful and interesting body of work.

Chapter 1. Duck nest survival in the Prairie Pothole Region relative to time-lagged spatial and temporal variation in environmental conditions [1]

Abstract

Populations in variable environments tend to respond to spatial and temporal variation in environmental conditions in a complex manner. Understanding variation in demographic rates is important for understanding population dynamics and developing effective conservation strategies. We studied variation in nest survival probability of upland-nesting ducks relative to landscape-level predictor variables describing spatial and temporal variation in current and recent environmental conditions. We hypothesized that nest survival would be related to both current environmental conditions and conditions in the previous two years. During 2002–2009, we monitored survival of 12,754 individually marked nests on 52, 10.4-km^2 study sites in the variable environment of the Prairie Pothole Region, USA. Selection among *a priori* models indicated that landscape-level nest survival was positively related to the number of wetland basins, current primary productivity, and current wetland conditions (i.e., drought status) and negatively related to primary productivity and wetland conditions during the previous two-years. The best-approximating model of nest survival estimated an approximately 12-fold difference in average probability of hatching for a mallard nest. For a given site and year,

[1] Prepared for submission to *Ecological Applications* as Walker, J., J. J. Rotella, S. E. Stephens, J. K. Ringelman, and M. S. Lindberg. Duck nest survival in the Prairie Pothole Region relative to time-lagged spatial and temporal variation in environmental conditions.

estimated nest success for 5 common species of upland nesting ducks ranged from 0.02 ($\hat{SE}$ = 0.01) to 0.23 ($\hat{SE}$ = 0.02), depending on the abundance of wetland basins and current and past primary productivity and wetland conditions. Because most duck nests that fail to hatch are destroyed by predators, we concluded that positive correlation of nest survival with current primary productivity and density of ponds and negative correlation with past primary productivity and wetland conditions indicated that short-term changes in precipitation were likely affecting the relationships between nest predators and nesting ducks in complex ways. These relationships might have been driven by pulses of productivity mediated by spatial variation in the abundance of highly productive wetland basins that had complex effects on nest predators and their prey, and in turn led to variation in nest survival. Our study is the first study, to our knowledge, that has clearly demonstrated a relationship between duck populations and relatively short-term pulses in productivity. We suggest that further investigation of these relationships could lead to a better understanding of the relative contributions of endogenous and exogenous influences to variability in duck populations.

Key-words: *Anatidae*, Daily Nest Survival, Demographic Rates, Landscape Ecology, Mallard, Primary Productivity, Resource Pulses, Reproductive Success

In variable environments, animal populations exhibit variation in demographic rates caused by spatial and temporal variation in limiting factors such as resource availability and predation (Sibly and Hone 2002, Meserve et al. 2003, Turchin 2003), and

identifying the sources of this variation is a basic goal of population ecology. Recent studies confirm the potential and demonstrated importance of spatial and temporal variation in environmental conditions to populations of a wide range of vertebrate taxa (e.g., Lobon-Cervia et al. 1995, Reaser 2000, Moynahan et al. 2006, Ozgul et al. 2006, Schwartz et al. 2006, Ozgul et al. 2007, Reid et al. 2008, Sibly et al. 2009). Variation in environmental conditions can exert a greater influence on populations than endogenous factors like density dependence (White 2008) or individual quality (Steiner et al. 2010). Understanding relationships between demographic rates and environmental variation in variable environments is therefore important both for increasing general knowledge of population dynamics and providing reliable information for managing populations.

When the environment is heterogeneous in both space and time, complex relationships between demographic rates and environmental conditions often result (Bissonette and Storch 2007). This complexity can arise from the combined effects of spatial and temporal variation in resource availabilty. For example, in a grazed, agricultural grassland system, first-year survival of a secondary consumer, the red-billed chough (*Pyrrhocorax pyrrhocorax*), is related both to availability of food among years and to quality of natal territory, but territory quality is more important in years with below average food abundance (Reid et al. 2008). Complex relationships between demographic rates and environmental conditions also manifest indirectly: often resonating through multiple tropic levels. For example, in deciduous forests with abundant mast-producing trees, availability of mast results in a rapid increase in small rodent populations, which in turn is associated with reduced predation on songbird nests,

nestlings, and adults (Schmidt and Ostfeld 2008). Further, complex, indirect relationships between demographic rates and environmental variation are often characterized by time-lags associated with the temporal scale of the response of different groups of species to environmental variation (Gunderson et al. 2007). For example, in a long-term study of plants and small rodents in a desert ecosystem, Thibault et al. (2010) showed that the time-lag associated with species-specific responses to variation in food resources induced by variation in precipitation increased with increasing trophic level. A search for generalities in complex, highly variable environments necessitates studies of adequate spatial and temporal extent to capture a representative range of variation in environmental conditions given the ecology and life-history of focal and interacting species (Gunderson et al. 2007, Hewitt et al. 2007, L. H. Yang et al. 2008).

Temperate grassland ecosystems are highly variable environments where both spatial and temporal variation in environmental conditions can have a strong influence on populations. Variability in precipitation, primary productivity, and land-use across multiple spatial and temporal scales characterizes these systems and results in substantial variation in resource availability (Samson and Knopf 1996, Y. Yang et al. 2008, Fornara and Tilman 2009, Millett et al. 2009). The Prairie Pothole Region (PPR) of North America is a temperate grassland ecosystem with an environment that is defined by spatial and temporal variation in the density of glacially formed, palustrine wetlands (van der Valk 1989), intensity of agricultural land use (Johnson et al. 1994), precipitation (Millett et al. 2009) and primary productivity (L. H. Yang et al. 2008). The PPR is an important breeding region for large populations of migratory birds (Sauer et al. 2008),

and reproductive success of migratory birds in the highly variable environment of the PPR is subject to proximate limitation through depredation of nests, young, and breeding females by generalist mammalian predators (Sargeant et al. 1993).

We conducted an extensive study of nest survival probability, an important demographic rate of upland-nesting dabbling ducks (*Anas* spp.) in the PPR, and related nest survival to landscape-scale spatial and temporal variation in environmental conditions. Past studies of nest survival of ducks in the PPR have often been relatively short duration (2yrs–5yrs) and focused on relationships of nest survival to landscape-scale spatial variation in land use (Greenwood et al. 1995, Reynolds et al. 2001, Horn et al. 2005, Stephens et al. 2005). Spatial and temporal variability in precipitation across the PPR has the potential to create considerable variation in primary productivity and wetland conditions (drought status) as the system oscillates between periods of wetness and drought. We thought variation in primary productivity and wetland conditions might have strong indirect effects on survival of duck nests through effects on nest predators, the overall prey base, or both (L. H. Yang et al. 2008). The objectives of our study were 1) to assess support for hypotheses about the relationships of nest survival to spatial and temporal variation in land use, wetland density, primary productivity, and drought status of wetlands and landscapes and 2) to evaluate whether nest survival was related to spatial and temporal variation in current and recent (previous 1-2 years) primary productivity and wetland conditions in a manner consistent with the hypothesis that pulses of primary productivity and wetness might be indirectly affecting duck populations (specific predictions are presented in *Methods*).

Methods

We studied nest survival probability of blue- winged teal (*Anas discors*), gadwall (*A. strepera*), mallard (*A. platyrhynchos*), northern pintail (*A. acuta*), and northern shoveler (*A. clypeata*) in the PPR of North and South Dakota, USA during 2002–2009 (Our study area was centered approximately 12km west of Turtle Lake, ND at: 101° 02′ 40″ W, 47° 31′ 35″ N). Formed during the late-Wisconsin glaciation approximately 10,000 ybp, the PPR (Fig. 1) is a 700,000-km^2 region in the North American midcontinent that is defined by its high densities of palustrine wetland basins (van der Valk 1989). The environment of the PPR is variable across spatial scales ranging from a few hundred meters to hundreds of kilometers and temporal scales ranging from weeks to centuries (Johnson et al. 1994, Shapley et al. 2005, Millett et al. 2009). The climate of the PPR is continental temperate with periods of extreme wetness and drought that vary in duration (Shapley et al. 2005, Millett et al. 2009, Niemuth et al. 2010). This region has undergone extensive land-use change during the past 150 years. A substantial proportion of the landscape has been converted from native grassland vegetation to cultivated cropland, the natural fire regime has been suppressed, and native flora and fauna have been affected by agricultural practices (Samson and Knopf 1996). Contemporary landcover of the PPR comprises native and introduced vegetation types. Land-use intensity is variable, ranging from annually cultivated cropland to idled perennial grasslands (Johnson et al. 1994). In this spatial context, wet-dry cycles drive variation in ecosystem productivity across the region (Y. Yang et al. 2008, Fornara and Tilman 2009).

The physiography of our study area was characterized by moderate relief (30m-90m), glacial soils, and high densities of wetland basins (Bluemle 1991). Landcover was a mosaic of perennial grassland and cultivated cropland. Typical land-uses were cattle grazing, annual cropping (both small grains and row crops), and forage production (Johnson et al. 1994). Low but chronic rates of grassland (0.6%/year to 1.5%/year; Stephens et al. 2008) and wetland (0.025%/year; United States Fish and Wildlife Service, Unpublished Data) conversion were observed across the study area during the study period. Seasonal temperatures and annual precipitation were highly variable (Millett 2009), and wetland conditions were dynamic among years of wetness and drought (Zimpfer et al. 2009).

Blue- winged teal, gadwall, mallard, northern pintail, and northern shoveler are the most numerous and widespread species of upland-nesting ducks in the PPR. In their various life stages from eggs to adults, these species provide abundant prey for a diverse suite of predators and are consumers of aquatic invertebrates, wetland vegetation, and grain from agricultural operations (Baldassarre et al. 1994). During our study, these species were the most abundant breeding duck species in our study area (Zimpfer et al. 2009). The breeding ecology and life history of upland-nesting ducks is consistent with the variable environment of the PPR. These relatively short-lived, long-distance migrants combine high breeding probability, early age at first breeding, and large clutch size with the ability to disperse distances ranging from tens of meters to hundreds of kilometers within and among breeding seasons (Johnson and Grier 1988, Johnson et al. 1992, Clark and Shutler 1999). Observed population size of these species is highly variable among

years and is related to spatial and temporal variation in the availability of wetland habitat (Viljugrein et al. 2005, Saether et al. 2008) and land-use practices (Miller 2000, Podruzny et al. 2002). Based on data from the widely distributed and heavily studied mallard, it appears that reproductive success determines most of the observed variation in population growth of upland-nesting ducks and that variation in nest survival probability determines most of the observed variation in reproductive success (Hoekman et al. 2002). Studies of spatial and temporal variation in nest survival probability are therefore thought to have a direct link to population dynamics in these species.

Survival probability of duck nests in the US PPR tends to be low (average ≈ 0.10–0.25) and variable (Drever et al. 2007). Most nest failures are caused by predators (Cowardin et al. 1985, Pieron and Rohwer 2010). Generalist mammalian predators are thought to have the most influence on nest survival probability (Sargeant et al. 1993, Pieron and Rohwer 2010). Coyote (*Canis latrans*), red fox (*Vulpes vulpes*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and American badger (*Taxidaea taxus*) are the most common known mammalian predators of nests and nesting female ducks in the region (Sargeant et al. 1993).

We collected nest data on randomly selected study sites using standard, systematic nest-searching techniques (Klett et al. 1986). Field crews searched for nests on 52, 10.4-km^2 study sites (approximately 3.2km by 3.2km) selected according to a sampling design stratified on two factors: 1) the proportion of perennial grass cover in a 41.4-km^2 area including and immediately surrounding the site and 2) the count of wetland basins on the 10.4-km^2 site. Spatial scales were based on the results of Stephens et al.

(2005). Proportion perennial grass cover and count of wetland basins on potential study sites was calculated using ArcGIS 9.3 (ESRI 2008) and United States Fish and Wildlife Service classified landcover (United States Fish and Wildlife Service, Unpublished Data). Sites were then randomly selected from the pool of potential study sites with the objective of maintaining a sample of 9–27 sites during every year of the study. Within each year, up to 30% of the sites were new sites that were used for just that year of study to add information about spatial variation in nest survival relative to landscape-scale environmental conditions.

All-terrain vehicles and standard, systematic nest-searching techniques were used to locate duck nests (Klett et al. 1986). Nest-searches were conducted from 0700 hr to 1400 hr during late-April through early-July (Klett et al. 1986, Gloutney et al. 1993). On each site, 3.3km^2-5.2km^2 representing 35%–100% of total grassland area on the site was completely searched for nests at least three times in each year that that site was included in the study. Cultivated land was not searched.

When a nest was found, we recorded date, species, number of eggs, and nest age. Nest age was determined by candling several eggs from each nest (Weller 1956). To aid relocation, the geographic coordinates of the nest were saved using a handheld Global Positioning Systems receiver and nests were marked by a fiberglass rod (1cm x 100cm) placed in the ground approximately 5m north of the nest. Marked nests were then revisited approximately every 5–7 days until the eggs hatched, were destroyed by a predator, were abandoned by the nesting female, or the nest failed for unknown reasons (Klett et al. 1986). Nest status (active or failed), stage of incubation, and apparent cause

given failure were recorded at each visit. Any nest that was abandoned by its attending female between the time when we discovered the nest and our next visit to the nest was excluded from analysis because of concerns that investigator activity may have caused the abandonment.

We used a model-selection approach (Burnham and Anderson 2002) to evaluate variation in nest survival relative to covariates describing variation in landscape-level environmental conditions among sites and among site-years. Specifically, we developed three sets of competing candidate models using covariates that described landscape-scale environmental conditions in terms of covariates that described 1) landscape-scale habitat covariates that were important to nest survival based on previous research and 2) spatially and temporally variable covariates that described spatial and temporal variation in primary productivity, wetland conditions (i.e., drought status of wetlands), and overall drought status of the landscape. The first two sets were devised prior to analysis and embodied a set of hypotheses about spatial and temporal variation in nest survival. The third set, which we considered more exploratory, was developed by combining features of the best-approximating models (in terms of a penalized likelihood; Burnham and White 2002, Link and Barker 2006) from the first two sets. We considered the full model and all nested models reasonable statistical hypotheses for the data, and we evaluated all possible subsets of variables in each set. The strategy of using separate candidate model sets to test hypotheses and arrive at a combined set of models therefore represented a compromise between *a priori* thinking and the frequently unmanageable potential size of model sets in large-scale ecological studies like ours (e.g., Reid et al. 2008). In our case,

reducing the number of models was important; the number of potential models was approximately 4,100 with all subsets of the covariates included.

We started our analysis with a base model that allowed nest survival to vary among the five species and incorporated a linear relationship between nest survival probability and nest age to avoid model misspecification due to potential species- and nest-level heterogeneity (Klett and Johnson 1982). We expected these sources of variation to be important, because of the consistent support they have received in past studies of nest survival of ducks in the PPR. Differences in nest survival among species might result from differences in nest-site selection or incubation behavior among species. Based on patterns observed in past studies, we predicted that blue-winged teal would have the highest nest survival probability and mallard would have the lowest (Stephens et al. 2005, Pieron and Rohwer 2010). Nest survival is positively related to nest age in many past studies (Klett and Johnson 1982, Emery et al. 2005, Stephens et al. 2005), possibly because nests that are placed in relatively secure locations tend to survive longer or because nesting females tend to spend more time at the nest as incubation advances and their nests are less likely to be depredated as a result. We predicted that nest survival would be positively related to nest age in our study. The base model thus included six parameters: an intercept term for each of the five study species and a slope term for nest age. This was the simplest model in the analysis, and it was nested within every model in every candidate set.

The first candidate model set was used to evaluate previously observed, scale-dependent relationships between nest survival and temporally static (on the scale of our

study), but spatially variable, environmental conditions. There were seven covariate models in the first set. Covariates included in the first set were 1) the proportion of perennial grass cover in the 41.4-km^2 landscape immediately surrounding the study site, 2) the amount of edge between perennial grassland and cultivated cropland on the 10.4-km^2 study site, and 3) the count of wetland basins (wet or dry) on the 10.4-km^2 study site. We assumed these landscape variables were effectively static during the 8-year study period given the low average rate of grassland and wetland loss across the region (Stephens et al 2008). Spatial scales of the covariates were based on the results of Stephens et al. (2005) who found these combinations to be most appropriate in a previous investigation of nest survival that included some of the same sites used in this study. Based on the results of several studies, we predicted a positive relationship between nest survival and proportion of perennial cover (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005), a negative relationship between nest survival and grassland-cropland edge (Chalfoun et al. 2002, Stephens et al. 2004, Stephens et al. 2005), and a negative relationship between nest survival and number of wetland basins (Phillips et al. 2003, Drever et al. 2004, Stephens et al. 2005). Studies of predator distribution and behavior provided a possible mechanism to support these predictions. Surveys of predator occurrence and radio-telemetry studies of the behavior of individual predators indicate that the species composition and relative abundance of nest predators tends toward fewer species with larger home ranges in landscapes where large amounts of intact grassland remain (Sargeant et al. 1993, Sovada et al. 1995, Phillips et al. 2004), and

that nest predators forage most frequently in small, isolated patches of grass cover and around wetland margins (Kuehl and Clark 2002, Phillips et al. 2003).

The second set of candidate models described nest survival probability as a combination of three covariates describing spatial and temporal variability in primary productivity and drought status of wetlands and landscapes. There were three covariates evaluated at three temporal scales and thus 511 covariate models in the second set. The covariates described variation in environmental conditions that we predicted would be related to variation in resources on the study sites: 1) the abundance of wet basins in May, 2) a dimensionless index of wetness (including surface water and moisture content of vegetation) through the entire nesting season, and 3) an index of gross primary productivity. These variables were evaluated at the spatial scale of the study site (10.4 km^2) and at three temporal scales: the current year (t), the previous year (t-1), and two years previous (t-2). Spatiotemporally variable landscape covariates were evaluated during the current year as well as in each of the two previous years to represent predicted associations of nest survival with both current and past May pond density, wetness, and primary productivity. These relatively short time scales seemed an appropriate starting point given the life history and behavior of both the study species and the mid-sized, generalist mammalian predators that affect nest survival (Drever et al. 2004, Saether et al. 2008).

Our predictions about potential variation in nest survival associated with spatial and temporal variation in past and present environmental conditions were based on observed patterns of year-to-year variation in broad-scale, annual surveys of abundance

of breeding duck pairs and the ratio of young-of-the-year to adults in samples of ducks harvested annually by hunters in the US (Raftovitch et al. 2009, Zimpfer et al. 2009). They were also based on knowledge of spatial and temporal variation in productivity of the PPR ecosystem (van der Valk 1989, Drever et al. 2004, Shapley et al. 2005) and precipitation-driven ecosystems in general (Owen-Smith et al. 2005, Fornara and Tilman 2009, Thibault et al. 2010). Recent studies by Drever et al. (2004, 2007), provided comparable research on nest survival on which to base variable-specific predictions. Drever et al (2004) reported small declines in nest survival with greater density of May ponds in the current and previous year on sites without predator management. Much like ideas presented by those authors, our predictions about relationships between nest survival and spatiotemporally variable landscape covariates in the current year were based on ideas about interactions among predators, vegetation cover and overall prey availability. We predicted that if predators preferentially foraged around wetland basins that contained water in early spring (Phillips et al. 2003), then the relationship between nest survival and May pond density would be negative given that nests would on average be located closer to wetlands in landscapes with higher wetland density. We predicted that if prey availability was greater in years of high primary productivity and vegetation density was higher in years of high primary productivity then predation rate would be lower and the relationship between nest survival and primary productivity would be positive (Klett et al. 1988, Brook et al. 2008). Wetness was a more comprehensive season-long measure of surface water, soil moisture and moisture content of vegetation. We predicted that if it related mostly to maintained wetland density through the season

then nest survival would have a negative relationship with this variable in the current year. Large changes in productivity and wetness related to precipitation cycles frequently occur in the PPR (Murkin et al. 1997, Millet et al. 2009, Neimuth et al 2010). This spatiotemporal variation might affect populations of nest predators through changes in food availability and winter severity, and thus result in a change in nest survival. We predicted that if the numerical response of nest predators was positive during wet periods with abundant resources and negative during dry periods when resources were relatively scarce, then the relationship between nest survival and recent landscape conditions would be negative with the highest potential nest survival probability associated with the initial year of a wet period following drought.

To more fully assess the relationship of nest survival to spatiotemporal variation in landscape state, we formed a third and final set of models by combining the best model or models from the second set with the full model from the first set. Based on our hypothesis that nest survival was driven by complex variation in the environment, we predicted that these models would provide a better description of variation in nest survival probability than models from either of the separate sets.

Publicly available landcover data, aerial survey data, and satellite imagery was used to calculate site- and year-specific values of covariates describing landscape state for input to statistical models. The proportion of upland area composed of perennial grassland cover in the 41.4-km^2 centered on the study site (PERCOV) and total amount of edge between perennial grassland and cultivated cropland on the 10.4-km^2 study site (EDGE), were calculated using United States Fish and Wildlife Service classified

landcover (United States Fish and Wildlife Service, Unpublished Data). National Wetlands Inventory (United States Fish and Wildlife Service 2010) data were used to count the wetland basins on each 10.4-km^2 study site (BASCNT). These covariates varied among sites, but were static among years. Covariates describing landscape conditions that varied among both sites and years were calculated using Moderate Resolution Imaging Spectrometer (MODIS) satellite imagery obtained from the National Aeronautics and Space Administration's Earth Observations Data Portal and from May pond count data from the FWS cooperative breeding pair and habitat survey (Smith 1995). Gross Primary Productivity (GPP; Reeves et al. 2006) and surface reflectivity were calculated and summarized from MODIS data collected at 8-day intervals. GPP provided an index to the amount of vegetation growth on a given site and year. Surface reflectivity was used to calculate the Normalized Difference Wetness Index (NDWI) which described combined surface water, soil moisture and water content of vegetation (Gao 1996). For a specific site-year combination, GPP was calculated as the maximum of the GPP measurements and NDWI was calculated as the sum of the NDWI measurements during April-July on the 1-km^2 MODIS pixel nearest the center of the study site. Segment-level (~4.45 km^2) May pond counts were downloaded from the USFWS Division of Migratory Bird Management Migratory Bird Data Center and used to calculate an inverse-distance-weighted value of wet pond density in May (PONDS) for each site in each year. ERDAS Imagine 9.3 (ERDAS 2008), ECognition 7.0 (Definiens Developer 2007), and the spatial analyst extension in ArcGIS 9.3 (ESRI 2008) were used to calculate values of covariates. To facilitate estimation of parameters in logit-scale

survival models, we scaled covariates to similar magnitudes by dividing by powers of ten. To assess possible multicollinearity among the covariates, we examined pair plots, correlation matrices, and Variance Inflation Factors (VIF) of the covariates with the AED package (Zuur et al. 2007) in R 2.10.0 (R Development Core Team 2010).

We used sample data to calculate several summary statistics which provided a basis for comparison to other studies and for model selection. Specifically, we calculated the proportion of nests in the sample by species, the proportion of failed nests that were destroyed by predators, the proportion of failed nests that were abandoned between discovery and the first visit, and the effective sample size. Effective sample size was calculated as the sum of 1) the number of days that nests were known to have survived and 2) the number of visit intervals that ended in failure (Rotella et al. 2004).

Nests were found at various ages, and re-visit intervals varied in length. We therefore used Daily Nest Survival (DNS) probability (Mayfield 1961) as the response variable in our analyses. Specifically, we employed a generalized linear model with binomial errors and logit-link function to estimate the log-odds (logit) of DNS as a linear function of the various combinations of the covariates described by the candidate models: that is, $\text{logit}(\text{DNS}_{ij}) = \log\left(\frac{\text{DNS}_{ij}}{1-\text{DNS}_{ij}}\right) = \beta_0 + \Sigma_k \beta_k x_{ijk}$ where the betas represented coefficients to be estimated and the x_{ijk} represented nest(i)- and day(j)-specific values of the k covariates (Dinsmore et al. 2002, Stephens 2005). Model coefficients and log-likelihoods were estimated using the nest survival module (Dinsmore et al. 2002) in

program MARK 6.0 (White and Burnham 1999) via R 2.10.0 (R Development Core Team 2010) and the contributed R package RMark 1.9.6 (Laake 2010).

The logit-linear model of DNS with binomial errors is valid assuming the following conditions (Dinsmore et al. 2002): 1) nests are correctly aged when discovered, 2) nest fates are determined correctly, 3) nest visits do not influence survival, and 4) nest fates are uncorrelated and constant for a given set of conditions specified by the covariates and model structure. Nests were correctly aged in this study. Candling techniques are effective for the study species (Weller 1956, Klett et al. 1986), and estimated nest age derived from candling was consistent with hatch date of observed nests in this study. Errors in classification of nest fate were probably rare because the study species leave conspicuous evidence of hatching in the form of detached embryonic membranes, and destroyed nests were easily identified by the presence of broken, partially consumed eggs and disturbed nest materials (Klett et al. 1986). To avoid influencing survival, we scheduled nest visits in the afternoon when females were likely to be absent (Gloutney et al. 1993), and visits were short in duration (< 5min). Observers were instructed to approach nests from various directions to avoid creating trails to nests. Nests that were abandoned between discovery and the first visit were not included in the analysis. As is common in studies employing generalized linear models, the fourth assumption, which relates to extra-binomial variation (overdispersion) and missing covariates (apparent overdispersion), was more challenging to address. Computationally practical, unbiased solutions for identifying and adjusting for overdispersion and missing covariates do not yet exist for large nest-survival datasets (Dinsmore et al. 2002, Rotella

et al. 2007). As an alternative, we evaluated the fit of the overall best-approximating covariate model relative to a general model with a separate estimate of DNS for each site in each year by using the heuristic method described by Shaffer and Thompson (2007). Specifically, we compared the estimates of DNS from a model with an estimated parameter for average DNS on each site in each year to the site-year level estimates of average DNS from the best-approximating model composed of covariates that described landscape state and looked for major, systematic departures of the model. We also estimated pair-wise correlation coefficients and VIFs for the variables in the overall best-approximating covariate model.

We used an information-theoretic approach to identify best-approximating models within and among candidate sets (Burnham and Anderson 2002). Posterior model weights calculated from Schwarz' Bayesian Information Criterion (BIC) provided the basis for discrimination among competing models (Schwarz 1978, Link and Barker 2006). We assumed equal prior probabilities for candidate models and considered the set of models that comprised 95% of the posterior BIC weight to represent the most plausible subsets of the covariates. We used the BIC because it is useful for selecting models that effectively balance the tradeoff between simplicity and realism in large, complex datasets like ours (Link and Barker 2006).

To evaluate the ecological significance of covariates and covariate combinations, we compared functions of DNS, such as estimates of 35-day nest survival probability (hereafter nest success; Klett et al. 1986) and ratios of maximum to minimum predicted nest success (Agresti 2007; 27), calculated from the model with the most posterior

weight. We used mallards as the basis of comparison to other studies as they are one of the most common and well-studied breeding ducks in the PPR. Estimates of DNS for each day of the nesting period ($\hat{DNS}_i$) were calculated using the estimated intercept for mallards, the age of the nest, and the site-year-level covariate conditions. The average mallard nest is exposed to mortality for 35-days between initiation and hatching (Klett et al. 1986). Estimated nest success for a mallard nest on a specific site in a specific year was therefore calculated as $\hat{NS}_i = \prod_{j=1}^{35} \hat{DNS}_{ij}$ where i indexed site-year and j indexed nest age. Ratios of estimated nest success at the maximum and minimum of each covariate with other covariates held constant at their medians provided an assessment of the potential change in nest success given the full potential range of variation (Agresti 2007). We also generated estimates of nest success with the observed covariate values for each site-year to provide an assessment of the range of variation in estimated nest success given realized variation in environmental conditions. Sampling variances of both nest success and ratios of nest success were estimated by the delta method (Seber 1982; 7, Williams et al. 2002; 736).

Results

We sampled 52 unique study sites for 161 site-years during 2002-2009. Number of sites sampled per year ranged from 9 to 26. Number of years per site ranged from 1 to 8, and 25 sites were sampled in 2 or more years. We located and monitored 12,754 nests which resulted in an effective sample size of 123,935. The most common nesting species was mallard (30% of the sample) followed by blue-winged teal (26%), gadwall (26%),

northern shoveler (10%), and northern pintail (8%). Approximately 90% of failed nests exhibited evidence of destruction by predators. Less than 2% of failed nests were associated with abandonment between discovery and the first visit. Landscape state was variable among sites and years (Table 1). The maximum VIF for any covariate was 3.13, and the full set of covariates was retained for use in candidate models.

The first set of candidate models described nest survival as a function of spatially variable environmental conditions measured at the landscape scale. This model set indicated that nest survival was related to BASCNT, but not PERCOV or EDGE. There was no support for our *a priori* predictions about relationships between nest survival and this group of covariates; the best-approximating model from this set contained only BASCNT and the estimated coefficient was positive ($\hat{\beta} = 0.056$; $\widehat{SE} = 0.013$)), which was opposite of our predictions. This model received 0.95 of the posterior weight in the set (Table 2). The 6-parameter base model received more posterior weight (0.03) than all of the candidate models that included PERCOV and EDGE. Models including PERCOV and EDGE received essentially no support (sum of posterior weight for the remaining 6 models = 0.02).

In contrast to the results for the first set, results from the second model set, which described nest survival as a function of both spatial and temporal variation in environmental conditions, were broadly consistent with several of our hypotheses and predictions but contradicted others. Three models received 95% of the posterior weight in this set (Table 3). The highest-weighted model (posterior weight = 0.81) included $PONDS_t$, $PONDS_{t-2}$, GPP_t, GPP_{t-2}, and $NDWI_{t-1}$. Contrary to our predictions,

relationships between DNS and these variables were consistently positive in the current year. Consistent with our predictions, relationships between DNS and the covariates were negative in past years. The other two models in the 95% set (combined posterior weight = 0.14) were similar to the top model in terms of structure and number of parameters, but revealed some uncertainty about GPP_{t-1}, and $NDWI_{t-2}$. GPP_{t-1} was included in both of these models. $NDWI_{t-2}$ was included in one (posterior weight = 0.05).

Comparison of the first and second model sets indicated more support for models of nest survival relative to current and recent spatial and temporal variation in landscape-level wetland conditions, wetness, and primary productivity than for models describing nest survival in terms of the proportion and configuration of perennial grass cover or the count of wetland basins in the landscape. The BIC difference between the top model from the first set and the top model from the second set was 126 units in favor of the top-ranked model from the second set. This result, although somewhat unexpected, was unequivocal.

The combination of spatially variable and time-lagged, spatially and temporally variable covariates provided substantial improvement.. When the 7 models from the first set were combined with the top 3 models from the second set, the resulting model set comprised 21 additional models (hereafter: combined set). The top-ranked model in the combined set represented a decrease in BIC of 52 units from the best model in the first set and 8 units from the best model in the second set. Although there was some model selection uncertainty within the combined set (Table 2), we chose to present detailed results for and base inference on the model with the greatest posterior weight for several

reasons. The utility and feasibility of model averaging was limited given our objectives, data, and models; patterns among coefficients and estimates were similar among models; and all covariates in the top model were included in at least 2 of the top three models (combined posterior weight = 0.80–0.86). Negative coefficients for past NDWI variables were nonetheless included in two of the top three models and these models received 34% of the posterior weight. This model selection uncertainty indicated that part of the ecological response of nest predators to variation in past landscape conditions was likely related to this season-long measure of wetness. The magnitude and direction of coefficients in the highest-ranked combined model (posterior weight = 0.66) was similar to the same coefficients in other models (Table 3) and generally supported our hypotheses about nest survival and landscape state. DNS was positively related to BASCNT, GPP_t, and $PONDS_t$ and negatively related to GPP_{t-1}, GPP_{t-2}, and $PONDS_{t-2}$ (Fig 2).

Analysis of probability ratios from the best-approximating combined model indicated that nest success was less strongly related to the number of wetland basins on a site than to current and recent variation in primary productivity and May pond density. When a single covariate was changed from its minimum to its maximum value and other covariates were held constant at their median values, ratios of maximum to minimum nest success ranged from 1.7 to 13.9. Estimated nest success ($\hat{NS}$) varied by a factor of 1.7 ($\hat{SE}$ = 0.2), over the observed range of BASCNT. Across the observed range of gross primary productivity in the current year (GPP_t), $\hat{NS}$ varied by a factor of 4.4 ($\hat{SE}$ = 0.9). Over the observed range of wet pond density in the current year ($PONDS_t$) $\hat{NS}$ varied by

a factor of 2.9 ($\widehat{SE}$ = 0.5). Estimated nest success varied by factors of 2.1 ($\widehat{SE}$ = 0.4), 2.3 ($\widehat{SE}$ = 0.4), and 13.9 ($\widehat{SE}$ = 5.0) over the observed range of GPP_{t-1}, GPP_{t-2}, and $PONDS_{t-2}$. Graphical comparison of mean DNS estimates from the 161-parameter, site-year model with estimates from the test model containing the best-approximating subset of landscape covariates indicated that the highest-weighted combined model of DNS provided informative site-year-level estimates of DNS with 6 parameters (Fig. 3).

The covariates in the best-approximating, combined model were correlated, but VIFs were less than 2.00 in all cases. The largest estimated correlations between covariates were between GPP_t and GPP_{t-2} (r = 0.60; 95% CI = 0.49, 0.69) and $PONDS_t$ and $PONDS_{t-2}$ (r = 0.57; 95% CI = 0.46, 0.67). Primary productivity was positively correlated with wetland abundance and wetland condition. The estimated correlation of GPP_t with BASCT was 0.30 (95% CI = 0.15, 0.43). GPP_t was also positively correlated with $PONDS_t$ (r = 0.24; 95% CI = 0.09, 0.38). Given the observed correlations among the lagged covariates, we were interested in empirical variation in estimated nest success during our study. We therefore examined the range of $\widehat{NS}$ given the combinations of the covariates associated with each site-year combination. Estimated nest success for a mallard varied by a factor of 11.9 ($\widehat{SE}$ = 3.3) among the 161 site-years in the sample. Minimum $\widehat{NS}$ of 0.02 ($\widehat{SE}$ = 0.01) was estimated for a site where pond density and primary productivity had both declined by 25% over two years. Maximum $\widehat{NS}$ of 0.23 ($\widehat{SE}$ = 0.02) was estimated for a site where pond density had increased by 230% and primary productivity had increased by 21% over two years. This result was broadly

consistent with our earlier analysis of probability ratios using the full range of the covariates.

Discussion

Our research on duck nesting in the PPR provided compelling evidence of relationships between an important demographic rate and complex spatial and temporal variation in environmental conditions. Rigorous analysis of our extensive data set revealed that nest survival probability was much more strongly associated with spatial and temporal variation in current and recent primary productivity and wetland conditions than with spatial variation in the density of wetland basins or with spatial variation in the amount and configuration of perennial grass cover in the landscape. Additional analysis indicated that spatial variation and spatial and temporal variation in environmental conditions were both important. Our results contributed to population ecology and wildlife management in both general and regional contexts. They provided another example of the importance of spatial and temporal variation in environmental conditions to the dynamics of vertebrate populations. Our results further demonstrated the importance of temporal scale by emphasizing the association of past conditions with a current response. Most generally, our results contributed to knowledge of resource pulses by describing a complex, wetland-mediated response to productivity in a temperate grassland system. Finally, by providing evidence that past environmental conditions were an important correlate of nest survival probability of upland nesting ducks in the PPR, our results provided new knowledge with important regional implications for future research and management.

In many populations, variation in environmental conditions that affects demographic rates often isn't strictly spatial or temporal: it is spatiotemporal (Turchin 2003). As a result, consideration of both the spatial and the temporal scale at which environmental conditions vary becomes important (Gunderson et al. 2007). Time lag dynamics are often viewed in an endogenous context and at very broad spatial and temporal scales (Bull and Bonsall 2008, Millon and Bretagnolle 2008), but there is reason to suspect that in some systems spatiotemporal variation in environmental conditions can produce responses at less-extensive scales (Schmidt and Ostfeld 2008, L. H. Yang et al. 2008). Studies of relationships between demographic rates and recent variation in environmental conditions often focus on long-term, large-scale climate drivers (Stenseth et al. 2003, Sandvik et al. 2005, Morrison and Hik 2007). We observed relationships between nest survival probability and recent variation in primary productivity and wetland conditions at a relatively small spatial scale (10.4 km^2) and a relatively short temporal scale (1-2 years). On our study sites, nest survival was positively correlated with current primary productivity and density of ponds but negatively correlated with past levels of these variables indicating that short-term changes in precipitation were likely affecting relationships between nest predators and nesting ducks in complex ways. The support we observed for combined models further indicated that these relationships might have been driven by pulses of productivity mediated by spatial variation in the abundance of highly productive wetland basins (Murkin et al. 1997, Anderson et al. 2008).

The effect of resource pulses is most well-studied in desert ecosystems (L. H. Yang et al. 2008, Thibault et al. 2010), but our research indicates that these concepts might also be relevant to the wetland-grassland ecosystem of the PPR. The patterns of variation that we observed suggest that pulses of wetness and productivity in this ecosystem have the potential to produce a strong effect on duck production through complex interactions between productivity, nest predators, and nesting ducks. Our study indicated that highest nest survival probability was associated with site-years where a location with abundant wetland basins was transitioning from dry conditions to wet conditions. When a change in wetland conditions was accompanied by a change in productivity then even higher predicted nest survival resulted. This pattern has characteristics of responses to resource pulses in other ecosystems (Schmidt and Ostfeld 2008), but we think that the unique feature of the PPR is the potential for amplification of spatiotemporal variation in productivity by local wetland communities. Further study of relationships between the demographic rates of upland nesting ducks and spatiotemporal variation in pulses of productivity might help to resolve uncertainty about the relative contributions of endogenous and exogenous forces to population dynamics in these species (Saether et al. 2008).

Variables that describe spatial heterogeneity in environmental conditions have been well-supported covariates in past studies of duck nest survival in the PPR (e.g., Greenwood et al. 1995, Reynolds et al. 2001) including a study based on two years of sampling on some of the same sites sampled in this study (Stephens et al. 2005). The number of wetland basins on a study site was included in our best-approximating

combined model, but the direction of the observed relationship was inconsistent with our predictions. Based on previous information about predator behavior (Phillips et al. 2003), we had predicted that nest survival would be negatively related to the number of wetland basins in the landscape. The positive relationship between nest survival and number of wetland basins that we observed was unexpected and resisted a simple *post hoc* explanation in the context of our *a priori* hypotheses. We speculated that possibly nest predators, and thus nest survival, might have been affected by higher-order interactions among landscape characteristics and conditions. Wetland basins are the most productive natural feature of the PPR landscape (van der Valk 1989, Murkin et al. 1997), thus the number of wetland basins in a landscape is expected to be positively related to its potential productivity. Our observation of positive correlations between primary productivity and wetland abundance and primary productivity and wetland conditions was consistent with this idea and suggested that interactions between spatially and temporally variable aspects of landscape state might have responsible for the relationships that we observed. Perhaps increased productivity increased the overall availability of prey for nest predators and countered the negative effect of predators foraging near wetlands.

Covariates that described environmental conditions in terms of landscape composition and configuration (the proportion of perennial grass cover in the landscape and the amount of edge between grassland and cropland) provided much less information about nest survival than we expected based on past research in the PPR. Part of the discrepancy between our results and the results of past studies might have been related to

differences in duration. Most studies of nest survival range from 3 to 5 years in length and thus tend to focus on relationships between nest survival and landscape characteristics. These relationships diminished rapidly in our data as years accumulated despite the spatial extent of our study and deliberate dispersion of sites along the gradient of grassland cover and wetland basins. In an exploratory reanalysis where data were added sequentially by year, models including perennial cover and edge received almost no posterior weight (i.e., $W_{BIC} < 10^{-6}$) relative to models that accounted for past and present variation in primary productivity and wetland conditions as the number of years increased from 1 to 3. This pattern persisted as years 4-8 were added (J. Walker, unpublished analysis).

Contrary to predictions about predators foraging preferentially near wetland basins, nest survival was positively related to pond density in May of the current year. Pond density in May is also related to the depth and duration of the previous year's snow cover which is related to winter severity (van der Valk 1989). Survival in raccoon (Pitt et al. 2008) and red fox (Barto and Zalewski 2007) populations is negatively related to winter severity, and winter severity might also negatively impact populations of striped skunks (Gehrt 2005). Regardless of the particular cause, we observed no support for the idea that nest survival would be lower in landscapes with a high density of wet basins in early spring. The positive relationship between nest survival and current primary productivity was more consistent with our predictions, and we thought it might have been related to increased availability of resources for predators of duck nests. For example,

increased productivity might have been correlated with higher prey density leading to lower predation rates on duck nests (Ackerman 2002, Brook et al. 2008).

Relative to past work on nest survival of ducks in the PPR, the site-level "memory" of past conditions was the most novel result of our study. There was much less previous PPR-specific information to guide our thinking about these relationships, and thus we recommend further investigation. We suspect nevertheless that our results will be supported by additional testing in our system given their concordance with our predictions about populations of nest predators and productivity of ducks relative to wet-dry cycles in the PPR. Negative relationships with past conditions were generally stronger than positive relationships with present conditions. These relationships likely described several aspects of the tendency for predation risk on duck nests to change with periods of relative stasis in wetness and productivity. This effect might have arisen through numerical or functional responses of predator populations to 2-3 year periods of wet (or productive) and dry (or unproductive) conditions. The pattern of variation in nest survival that we observed was consistent with the hypothesis that predator populations responded to periods of abundance and scarcity of resources such that predation declined during periods of drought and increased during wet periods (Holt 2008, Schmidt and Ostfeld 2008).

We could not rule out the possibility that some of the results in our study were the result of within-population influences (Drever et al. 2004, Sæther et al. 2008). For example, unexpected positive relationships between nest survival and number of wetland basins and between nest survival and the current number of May ponds both might have

resulted from a positive, density-dependent effect on nest survival that resulted from a type II functional response (Holling 1966) of nest predators to increased abundance of nests on sites with more wetland habitat (Cowardin et al. 1985). Positive relationships between nest survival and present wetland conditions and productivity and negative relationships with recent wetland conditions and primary productivity might have resulted from a regional shift toward more-experienced, or higher-quality, individuals in the breeding population over relatively short time scales (Cam et al. 2002, Drever et al. 2004). We nonetheless think that environmental conditions were probably equally or more important to nest survival than endogenous influences given 1) the short life-span and proclivity toward dispersal observed in the migratory species that were the focus of our study (Lokemoen et al. 1990, Johnson et al. 1992) and 2) the potential for environmental conditions to affect the overall prey base (Brook et al. 2008) and populations of resident nest predators (Sargeant et al. 1993) that ultimately limit nest survival (Pieron and Rohwer 2010).

To our knowledge, our study is one of the most spatially and temporally extensive efforts to evaluate and understand reproduction of upland nesting ducks, and possibly the most well-replicated in space and time. Given the likely influence of nest survival probability on reproductive success and population dynamics of the study species, the results of our study had clear implications for the population dynamics of breeding ducks in the PPR and further affirmed the importance of wetland dynamics in this system. Density of breeding pairs is positively correlated with wet pond area in the spring (Reynolds et al. 2006). Nest survival probability was positively correlated with current

May pond density in this study. Survival of breeding females is positively correlated with nest survival because most mortality of breeding females is associated with depredation during nesting (Devries et al. 2003). Duckling survival probability is positively correlated with the amount of seasonal wetland habitat (Krapu et al. 2000, Pietz et al. 2003). Therefore, when a precipitation-driven pulse of increased wetland density and productivity occurs, the potential for a large increase in the population could be maximized. This hypothesis is consistent with a variety of independent data sources (e.g., Millett et al. 2009, Raftovitch et al. 2009, Zimpfer et al. 2009) and predicts that short-term cycles of wetness and productivity might produce most of the spatial and temporal variation in duck populations in the PPR. Another interesting implication resulted from the observed relationship between nest survival and current and recent wet pond dynamics. Nest survival was more sensitive to changes in wet pond density in May (the most variable predictor in the best- approximating model; Table 1) than to changes in primary productivity. The negative association between nest survival and past wetland conditions was stronger than the positive association between nest survival and current wetland conditions. When considered at the level of an individual, this result suggested that the potential range of successful nesting strategies might have been rather broad. Both site fidelity and breeding dispersal are common in the study species (Johnson and Grier 1988, Lokemoen et al. 1990), but the relationship of these choices to spatial and temporal variation in landscape state given likely trade-offs between pioneering a site and having knowledge of a site is relatively poorly known. A greater understanding of the

patterns and mechanisms of breeding dispersal in these species would provide useful information for both ecologists and conservation planners.

Conservation of North American duck populations is an ecologically and economically extensive enterprise (United States Fish and Wildlife Service and Canadian Wildlife Service 1986). The primary breeding range of these species, the Prairie Pothole Region, is defined by its variable environment (Shapley et al. 2005, Millett et al. 2009). Although much is known about the ecology of these populations, their large geographic range and the importance of precipitation-driven cycles and land-use practices on privately owned agricultural land to their dynamics make experimental manipulation of relevant factors at useful scales difficult or impossible. Extensive monitoring programs and observational studies have nevertheless made clear several themes that are relevant to the ecology and management of these populations. Population dynamics of waterfowl in the PPR are consistently correlated with the spatial and temporal dynamics of wetland habitat. Our study corroborated the potential importance of landscapes with high wetland density to breeding waterfowl. It also provided new insight about the potential effect of cycles of wetness and drought on the size of duck populations over time. Variation in landscape state induced by relatively short-term cycles had a consistent relationship to nest survival in our study. Patterns of wetness in the PPR are subject to considerable spatial and temporal variation (Royle et al. 2002, Neimuth et al. 2010). Habitat conservation strategies for these populations thus might be most effective when focused on protecting native grasslands and wetland basin habitat at extensive scales: for several reasons. The size and productivity of breeding duck populations is related to wetland

abundance, primary productivity, and wetland condition. The productivity of the PPR landscape is related to plant species diversity (Fornara and Tilman 2009) and wetland density (Murkin et al. 1997). Conservation of landscapes with intact native grassland communities and high densities of wetlands might be consequently an effective strategy to provide quality habitat for breeding ducks in the current environment of the PPR. The future stability of the PPR system is, however, somewhat less certain. Native grasslands in the PPR are currently undergoing chronic conversion (Stephens et al. 2008). Another challenge for duck populations will be the extent to which the changing global climate affects the wet-dry cycles that seem to define the productivity of the PPR landscapes and duck populations (Millett et al. 2009, Zimpfer et al. 2009). Current trends have been positive for ducks in the PPR, but little is known about potential changes in patterns of variation (Johnson et al. 2010). There is also much to be learned about whether correlations between reproductive success of ducks and landscape state are consistent throughout the PPR over longer time periods. Long-term measurement of reproductive output of these species at extensive scales would be useful to address questions related to climate and landscape change and to provide critical knowledge to managers and ecologists.

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Table 1.1 Summary statistics (mean, standard deviation [SD], quartiles) and Variance Inflation Factors (VIF) for landscape covariates used to parameterize models of daily nest survival probability of upland-nesting ducks.

Covariate[a]	Mean	SD	Min.	Q1	Median	Q3	Max.	VIF
BASCNT	186.00	89.00	10.00	132.00	177.00	259.00	374.00	1.22
EDGE	16340.00	11396.00	0.00	9205.00	11860.00	23830.00	47880.00	1.86
PERCOV	0.64	0.23	0.16	0.46	0.65	0.87	0.98	2.01
GPP_t	333.00	58.00	119.00	305.00	334.00	377.00	448.00	2.08
GPP_{t-1}	333.00	67.00	119.00	280.00	340.00	381.00	474.00	2.57
GPP_{t-2}	350.00	56.00	158.00	323.00	358.00	393.00	448.00	2.26
$NDWI_t$	-2.20	0.68	-3.92	-2.64	-2.21	-1.78	0.16	2.13
$NDWI_{t-1}$	-2.34	0.61	-3.84	-2.82	-2.27	-1.83	-0.68	2.39
$NDWI_{t-2}$	-2.15	0.58	-3.84	-2.47	-2.14	-1.79	-0.15	2.27
$PONDS_t$	9.81	5.55	0.94	6.32	8.64	12.03	36.10	1.93
$PONDS_{t-1}$	8.04	4.78	0.94	4.89	7.44	10.14	31.86	3.13
$PONDS_{t-2}$	8.63	4.52	0.94	5.74	8.28	10.97	31.86	3.05

[a]Definitions of covariate names: BASCNT was the count of wetland basins on the 10.4-km^2 study site, EDGE was the total length (m) of edge between perennial grassland and cultivated cropland on the study site, PERCOV was the proportion of upland area in 41.4-km^2 landscape centered on the study site composed of perennial grass cover, GPP was an index of the maximum gross primary productivity (gC/m^2) on the study site, NDWI was the sum of the Normalized Difference Wetness Index (Gao 1996) values measured weekly on the study site, and PONDS was a spatially interpolated index of the density of wetland basins ($basins/km^2$) containing water on the study site. BASCNT, EDGE, and PERCOV were temporally constant. GPP, NDWI, and PONDS varied in space and time and were evaluated for the current year and the two previous years. Variation among current and past values of GPP, NDWI, and PONDS was due to sites that were studied in a single year.

Table 1.2 Results of selection among three sets of candidate models of Daily Nest Survival probability (DNS) of upland nesting ducks relative to landscape state. Models listed within each candidate set represent at least 95% of the posterior weight (W_{BIC}) within that set. Covariate abbreviations are defined in Table 1.1.

Model Set	DNS Model	-2logL	Number of parameters[a]	BIC	W_{BIC}
Spatially Variable	BASCNT	37096	7	37178	0.95
Spatially and Temporally Variable	$PONDS_t + GPP_t + NDWI_{t-1} + GPP_{t-2} + PONDS_{t-2}$	36923	11	37052	0.81
	$PONDS_t + GPP_t + GPP_{t-1} + GPP_{t-2} + PONDS_{t-2}$	36927	11	37056	0.09
	$PONDS_t + GPP_t + GPP_{t-1} + GPP_{t-2} + NDWI_{t-2} + PONDS_{t-2}$	36917	12	37058	0.05
Combined	$BASCNT + PONDS_t + GPP_t + GPP_{t-1} + GPP_{t-2} + PONDS_{t-2}$	36903	12	37044	0.66
	$BASCNT + PONDS_t + GPP_t + NDWI_{t-1} + GPP_{t-2} + PONDS_{t-2}$	36905	12	37046	0.20
	$BASCNT + PONDS_t + GPP_t + GPP_{t-1} + GPP_{t-2} + NDWI_{t-2} + PONDS_{t-2}$	36894	13	37047	0.14

[a]Each model contained the 6 parameters of the base model: an intercept term for each of the five study species and a slope term for nest age.

Table 1.3 Estimated logit-scale coefficients and standard errors (SE) from three best-approximating models of daily nest survival probability of upland-nesting ducks relative to landscape characteristics and conditions. Covariate abbreviations are defined in Table 1.1.

	$W_{BIC} = 0.66$		$W_{BIC} = 0.20$		$W_{BIC} = 0.14$	
Covariate	Mean	SE	Mean	SE	Mean	SE
Blue-winged teal	2.619	0.086	2.307	0.107	2.399	0.114
Gadwall	2.508	0.088	2.191	0.109	2.281	0.116
Mallard	2.380	0.085	2.067	0.106	2.157	0.114
Northern pintail	2.538	0.093	2.224	0.113	2.311	0.120
Northern shoveler	2.532	0.091	2.214	0.112	2.305	0.118
Nest age	0.031	0.001	0.031	0.001	0.031	0.001
BASCNT	0.067	0.014	0.057	0.014	0.064	0.014
GPP_t	0.181	0.025	0.167	0.024	0.191	0.025
GPP_{t-1}	-0.099	0.023			-0.099	0.023
GPP_{t-2}	-0.138	0.028	-0.184	0.025	-0.129	0.028
$NDWI_{t-1}$			-0.083	0.021		
$NDWI_{t-2}$					-0.065	0.022
$PONDS_t$	0.354	0.057	0.372	0.056	0.376	0.057
$PONDS_{t-2}$	-0.668	0.069	-0.656	0.070	-0.632	0.070

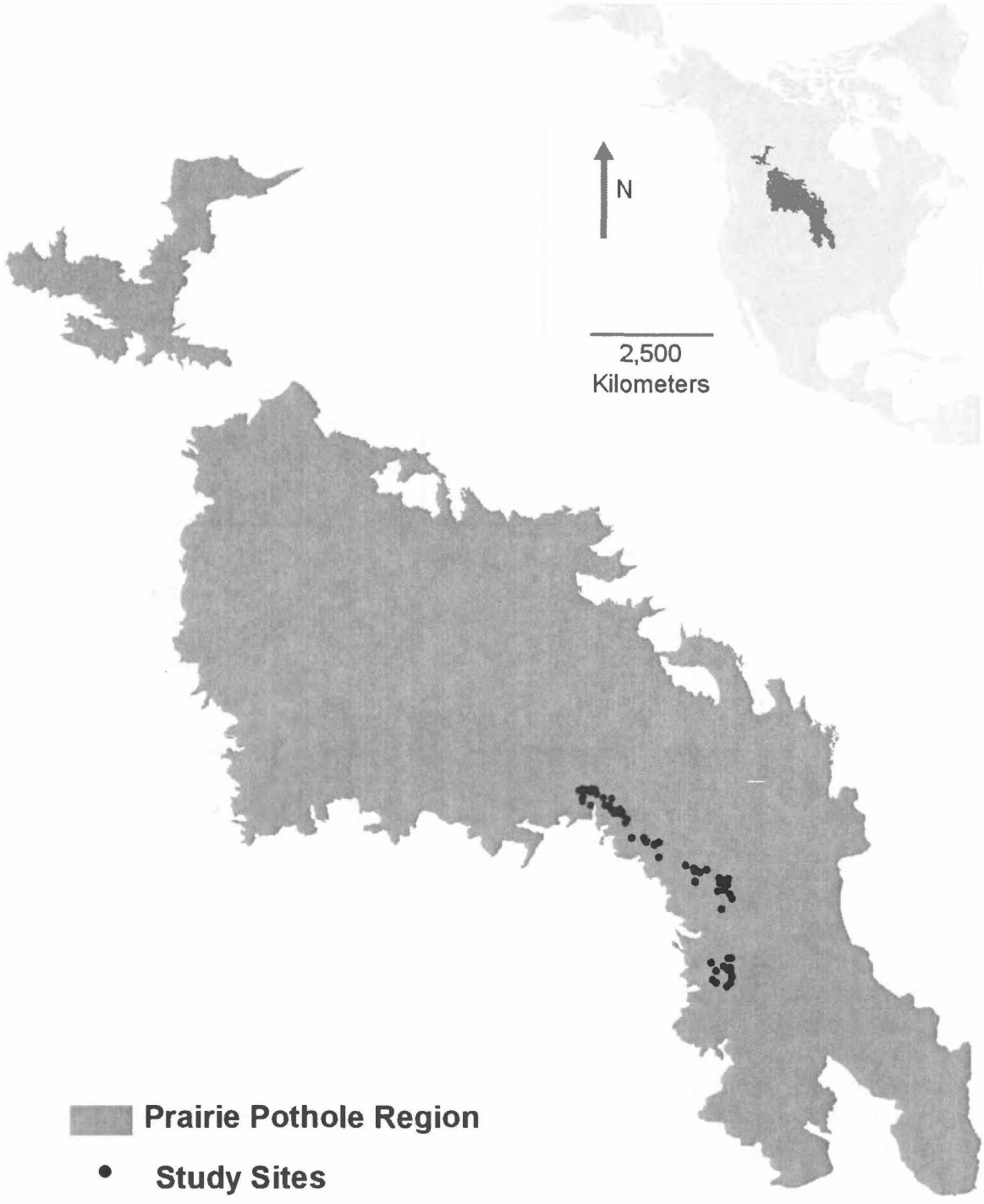

Figure 1.1 Location and extent of the Prairie Pothole Region in the U.S. and Canada and locations of study sites used for investigation of nest survival relative to environmental conditions.

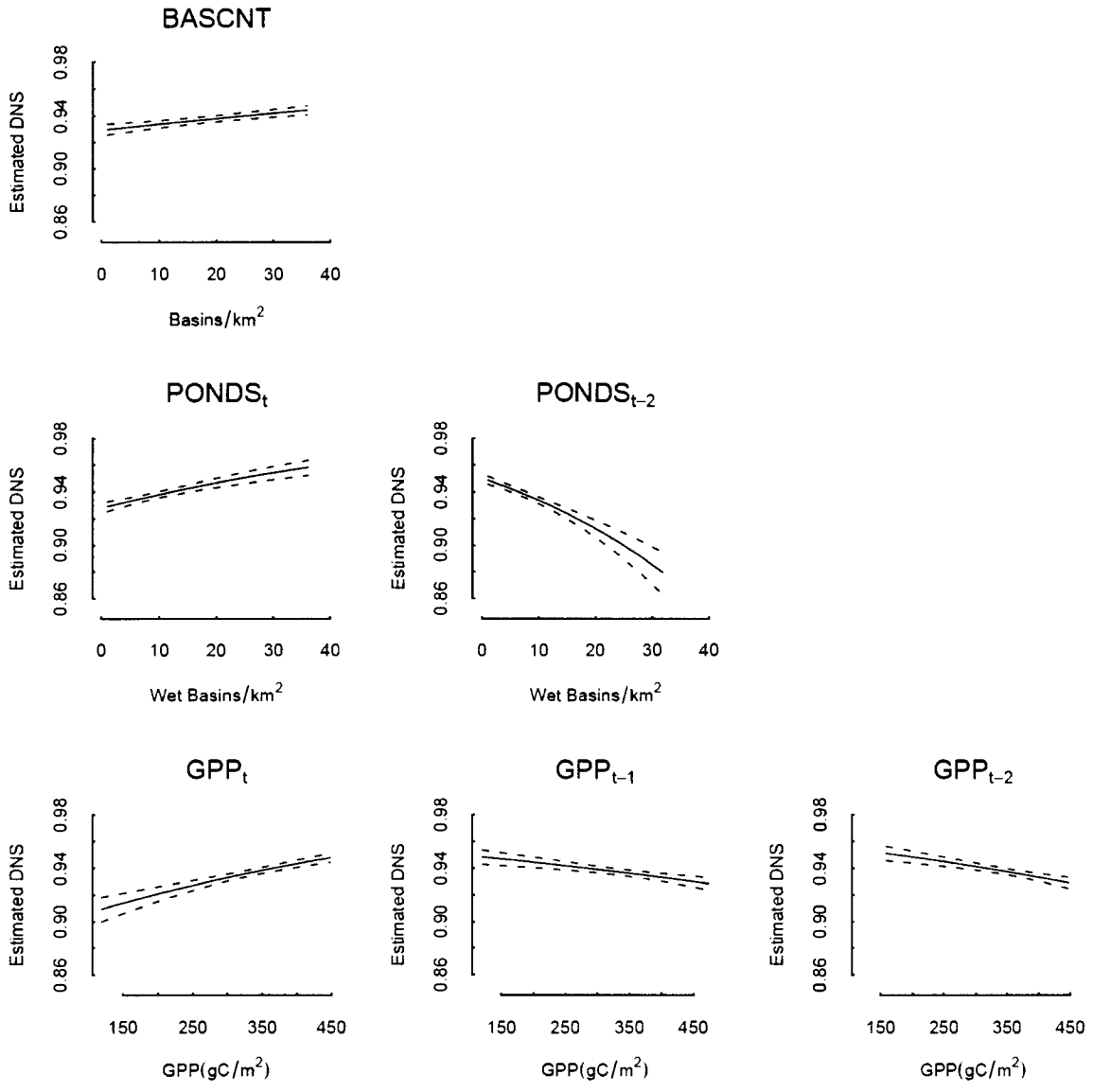

Figure 1.2 Daily Nest Survival probability (DNS) of upland-nesting ducks relative to covariates describing variation in environmental conditions among site-years. Solid lines represent mean DNS estimated for a mallard nest across the range of variation in the covariate with all other covariates held constant at their median values. Dashed lines are 95% confidence limits. Tick marks on the y-axes correspond to a range of nest success probability from 0.01 to 0.50 for the nesting period of a typical mallard (35 days). Covariate abbreviations are defined in Table 1.1.

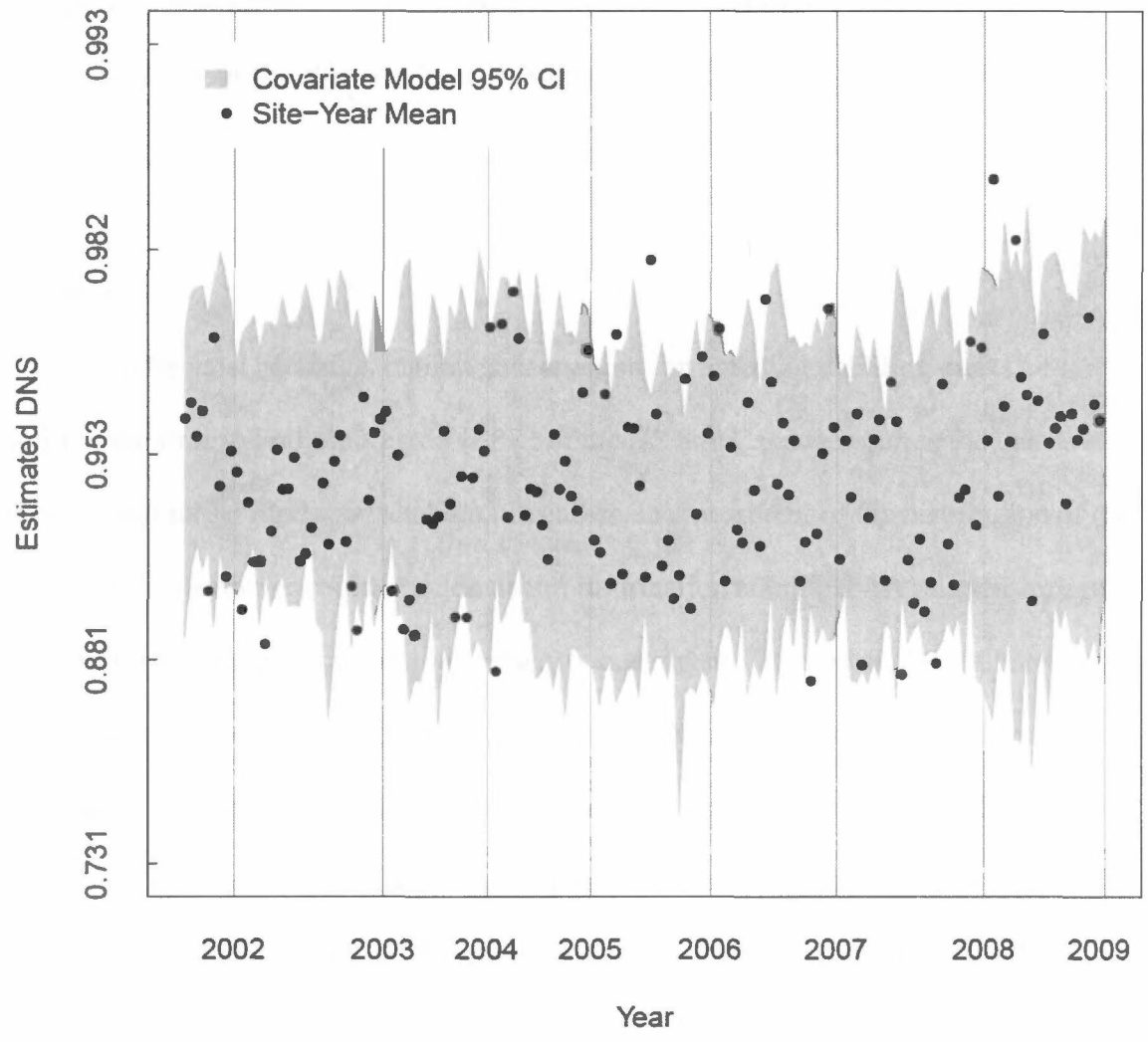

Figure 1.3 Estimates of Daily Nest Survival probability (DNS) from a 161-parameter model with a unique estimate for each study site in each year (points) compared to the estimated 95% confidence region of mean estimates (gray band) from a 7-parameter model of DNS that was a function of landscape covariates taken from the model with the highest posterior weight. Gray vertical lines represent transitions between years with points to the left of x-axis labels corresponding to sites sampled in that year.

Chapter 2. Occupancy of wetlands by duck broods relative to habitat characteristics in the Prairie Pothole Region[1]

Abstract

To be most effective, habitat conservation for breeding dabbling ducks (*Anas* spp.) in the Prairie Pothole Region (PPR) of the US and Canada requires the means to identify and target productive habitat. Broad-scale assessment of the distribution of duck broods in late-summer could provide useful information about habitat relationships of duck broods that would be complimentary to existing surveys and studies of breeding ducks. Broods are difficult to detect, however, rendering data from brood surveys difficult to interpret. Recent developments in sampling and analysis methods for occupancy surveys offer a solution to this problem: repeat-visit surveys combined with hierarchical statistical models. We conducted repeat-visit brood surveys on 3,226 wetland basins on 167, 10-4-km^2 study plots in the PPR during late-summer 2007-2009. We concluded that a repeat-visit, wetland based survey provided a useful and informative tool for identifying wetland basins and landscapes associated with higher probability of occupancy by broods. We observed relationships between wetland occupancy by broods and habitat covariates that were largely consistent among species and potentially useful for identifying important habitats. Probability of occupancy by a brood was greater on

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larger basins for all five study species and was greater on basins located on study plots with a higher proportion of perennial grass cover for four of five species. Using gadwall (*Anas strepera*) as an example, we observed that as wet basin area increased from 0.19ha to 2.12ha, median probability of a wetland basin being occupied by brood increased from 0.08 (90% Credible Interval: 0.07, 0.10) to 0.28 (0.24, 0.33). As proportion of perennial grass cover on the 10.4-km^2 study site increased from 0.03 to 0.99, probability of basin occupancy by a gadwall brood increased from 0.12 (0.09, 0.16) to 0.20 (0.16, 0.25). Consistent with past work, probability of detection was low and variable supporting the conclusion that this parameter needs to be dealt with directly during the design and analysis of brood surveys. Broods were detected on only 3% to 12% of wetland basins, but species-level estimates of probability of occupancy indicated that from 9% to 35% of basins were occupied. We concluded that our extensive brood survey provided useful information about the distribution of duck broods across a large geographic extent.

Key-words: *Anas*, brood distribution, detection probability, habitat conservation, habitat use, hierarchical models, mixed-effects models, reproductive success, recruitment, waterfowl populations

Effective conservation of wildlife populations requires a reliable means of evaluating habitat (Morrison et al. 2006). Relationships among habitat use, fundamental population parameters (i.e., abundance, survival, and reproduction), and habitat characteristics determine the value of habitat (Johnson 2007). These relationships can be

challenging to identify and characterize. Extensive studies of presence or abundance relative to habitat have long been criticized for lacking detail about demographic rates (Van Horne 1983), but detailed information about reproduction and survival relative to habitat is often available only at limited spatial and temporal extents and for a limited suite of demographic rates (Johnson 2007). These limitations provide motivation to seek out alternative approaches. Estimating the probability of occupancy of spatially distinct habitat patches relative to habitat characteristics could provide a rapid and possibly informative alternative assessment of habitat across a large extent (MacKenzie et al. 2006), and detail of occupancy studies can be increased by focusing on specific occupancy states (Nichols et al. 2007). For example, patch-scale occupancy of habitat by young-of-the-year individuals might provide evidence of successful reproduction that could provide information about relationships of reproduction and habitat use to habitat characteristics. Presence-absence data nevertheless need to be corrected for non-detection to provide interpretable estimates of probability of occupancy, and this requirement can diminish the utility of occupancy surveys (Gu and Swihart 2004, MacKenzie 2005). Recent developments in the application of hierarchical statistical models that facilitate concurrent estimation of probability of occupancy and probability of detection have made occupancy estimation a potentially more useful means of identifying important habitat (MacKenzie et al. 2006, Royle and Dorazio 2008). These developments have opened up new possibilities for using occupancy surveys to assess habitat relationships across large landscapes.

Habitat conservation for breeding dabbling ducks (*Anas* spp.) in the Prairie Pothole Region (PPR) of the north-central United States and south-central Canada is a multi-million dollar effort that depends in part on the accurate identification of productive habitat in a complex environment (United States Fish and Wildlife Service and Canadian Wildlife Service 1986, Williams et al. 1999). Extensive, long-term count surveys of breeding pairs relative to wetland characteristics and detailed, but more spatially, temporally, and demographically restricted, assessments of reproduction and survival currently provide the information basis for habitat conservation efforts in the PPR (e.g., Cowardin et al. 1995, Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005, Reynolds et al. 2006). Late-summer brood surveys potentially provide additional information for these efforts (Cowardin and Blohm 1992). Identification of wetlands and landscapes associated with the presence of broods might lead to new knowledge about relationships between populations and habitat. Occupancy of wetlands by broods provides evidence of successful nesting in the vicinity of occupied wetlands and information about the characteristics of wetlands that are used by broods. Within-year comparison of the distribution of breeding pairs with the distribution of broods could be another useful way to assess relationships between settling patterns and reproduction at broad extents.

Broods occupy small, spatially distinct wetland basins that can be rapidly surveyed, thus surveys of wetland basins potentially provide a basis for identifying those landscapes and basins that are associated with higher probability of occupancy by broods. However, because of the cryptic coloration, small size and secretive behavior of

ducklings, the probability of detecting a brood tends to be low (typically less than 0.5) and variable (Hammond 1970, Ringelman and Flake 1980). Thus, observations of broods that do not account for failed detections are not reliable indicators of which locations are occupied by broods.

Various approaches have been used to estimate detection probability of broods (Ringelman and Flake 1980, Rumble and Flake 1982, Cooper 1996, Giudice 2001, Pagano and Arnold 2009). Most of these survey methods were designed primarily to assess probability of detection rather than to allow assessment of habitat relationships. They generally have intensive sampling requirements and require that broods be individually marked. These approaches have consequently not been implemented at broad scales. Flexible hierarchical mixture models that facilitate simultaneous estimation of probability of occupancy and probability of detection of unmarked broods relative to covariates have recently become widely available (MacKenzie et al. 2006, Royle and Dorazio 2008) and can often be used with relative simple sampling approaches. These models have the potential to allow extensive assessment of habitat relationships while simultaneously controlling for variation in detection rate given repeated surveys of unmarked broods. We therefore expected that the combination of repeated surveys of wetland basins across the PPR and hierarchical mixture models would provide both a viable sampling approach and the analytical ability to examine habitat relationships of duck broods while accounting for detection. We conducted an extensive, repeat-visit survey of wetland basins in the PPR, recorded observed presence or absence of broods, and applied hierarchical occupancy models to the resulting data. We had three objectives

for our study: 1) to assess the utility of this approach for region-wide evaluation of habitat for duck broods, 2) to investigate predictions about ecological relationships between species-specific probability of occupancy and variables describing wetland and landscape characteristics, and 3) to account for relationships between detection probability of duck broods and covariates affecting visibility of broods. Specific predictions are presented in the *Methods* section.

Methods

Our study area was the PPR of North and South Dakota: essentially the area east of the Missouri River in these two states (Fig. 1). This area was characterized by high densities of wetland basins, heterogeneous land-cover and land-use, and large populations of migratory waterfowl (van der Valk 1989, Johnson et al. 1994, Zimpfer et al. 2009). Abundant, glacially formed wetlands were the characteristic ecological feature of the landscape and they attracted high densities of breeding waterfowl during years of adequate precipitation (van der Valk 1989, Zimpfer et al. 2009). Most land was in private ownership, and the most common land-uses were related to production of small grains, row crops, and beef cattle. Land cover was a mosaic of annually cultivated cropland, stands of introduced perennial grasses and forbs used for forage, perennial grassland used for pasture, and restored, mostly idled perennial grassland retired from cultivation under the US Department of Agriculture's Conservation Reserve Program. Climate, physiography, dominant land-uses, and ecology of the study area have been described in detail elsewhere (Johnson et al. 1994, Cowardin et al. 1995, Reynolds et al. 2006).

We focused our survey effort on the five most common breeding duck species in the PPR, blue-winged teal (*Anas discors*), gadwall (*A. strepera*), mallard, northern pintail (*A. acuta*), and northern shoveler (*A. clypeata*), and the three most common and important wetland classes for breeding waterfowl in the PPR: i.e., seasonal, semipermanent, and temporary wetlands (Stewart and Kantrud 1971, Reynolds et al. 2006). Our study was conducted on 167, 10.4- km^2 study plots during 20 July–5 August 2007–2009. In past studies, this plot dimension roughly approximated the observed breeding season home range of radio-marked female mallards (Dwyer et al. 1979, Cowardin et al. 1995). Timing of our survey was intended to provide a representative cross-section of broods of the five study species and represented a compromise between the breeding chronologies of earlier- and later-nesting species (Klett et al. 1988, Cooper 1996). The majority (140) of the sampled plots were selected from the 384 plots that made up the US Fish and Wildlife Service (USFWS) Four-Square-Mile Survey (FSMS) sample frame in North and South Dakota. As part of an extensive, ongoing survey of density of breeding duck pairs, these plots were randomly selected in 1987 and 1990 from three strata that described areas with high, medium, and low proportion of land owned by the USFWS (Cowardin et al. 1995). We selected plots from the FSMS sample with the objective of surveying landscapes across a representative gradient of perennial grass cover and wetland basin density while minimizing travel time between plots. Another group of 27 plots where Ducks Unlimited, Inc. (DU) was conducting a simultaneous investigation of nest survival probability of ducks was included in the

sample during 2008 and 2009. The DU plots were selected randomly from two strata: proportion of perennial grass cover and number of wetland basins on the site.

We required a survey design that could be implemented across a large region by field assistants with a broad range of experience and training, thus we developed a relatively simple protocol for field data collection (Sewell et al. 2010). Each observer was provided a set of geo-referenced plot maps consisting of an aerial photo of each plot (United States Department of Agriculture 2010) overlaid with uniquely numbered National Wetlands Inventory (NWI; United States Fish and Wildlife Service 2010) wetland basin polygons. Public roads were buffered by a distance of 200 meters. Field surveys comprised three visits to each plot. All visits to a specific plot were conducted by the same observer. During each visit, the observer surveyed every NWI wetland basin that contained visible water and intersected the 200-meter buffer. All surveys were conducted from roadsides, and observers remained in the vehicle during the survey. Visits were conducted over a roughly 24-hour period consisting of a morning, afternoon, morning or an afternoon, morning, afternoon survey sequence. Observers used binoculars and spotting scopes to survey the visible portion of each wetland basin and remained at each basin for two minutes or until all broods had been observed and recorded. The species, age class, and number of ducklings of each observed brood was recorded. If no broods were observed, then observers recorded a zero. They also recorded several variables describing the survey replicate and the wetland basin. Date, time, and wind speed (Beaufort scale; Simpson 1926) were recorded at the beginning of each plot replicate. Observers recorded a subjective assessment of the proportion of the

surveyed wetland area obscured by emergent vegetation during the first replicate only. Types of vegetation were not differentiated. Observers who were employed as seasonal field assistants were given one day of training on the data collection protocol and 3-5 weeks of field practice. The remaining observers were permanently employed waterfowl biologists with experience doing brood surveys; they were given training on the protocol only. All observers used the same protocol for all surveys.

We used the wetland-basin-level survey data to estimate the probability of occupancy of a wetland basin by a brood (ψ) and the probability of detecting a brood during a visit to a wetland basin (p). The distribution of broods among wetland basins during late summer is most likely a function of pair abundance, nesting chronology, nest survival rate, brood survival rate, and the use of available wetland basins by female ducks during the brood-rearing period. We hypothesized that variation in ψ would therefore be related to habitat characteristics that were related to the size and distribution of the breeding pair population and to the reproductive success and habitat use of breeding females. We hypothesized that variation in p would be related to covariates that described variation in the visibility of broods associated with brood behavior, age, and size; habitat characteristics; survey timing; and observer ability. We selected covariates based on their linkage to our hypotheses given existing knowledge of brood survey techniques and brood ecology.

Our hypotheses and predictions about ψ were based on knowledge of the abundance and distribution, breeding chronology, habitat-use, and reproductive success of the study species. Among species, we predicted that broods of blue-winged teal,

gadwall, and northern shoveler (later-nesting species) would be more numerous than mallard or northern pintail broods (earlier-nesting species) during the study period and thus would be associated with higher average ψ. Three visits to the wetland basins on a given plot were completed in 24-hours, but all 167 plots were not surveyed on a single date. Rather, plots were surveyed over a roughly two-week period. As a result, there was potential for ψ to change among plots over the 15-day study period given ongoing hatching, fledging, and mortality of broods. We predicted that ψ for broods of later-nesting species might increase during the study period due to additions of new broods from late hatched nests and that broods of earlier-nesting species might decrease during the study period due to losses of broods to mortality and fledging. We thought that basin vegetation might also affect ψ among species. Knowledge of species-specific habitat-use indicated that gadwall, northern shoveler, and northern pintail might be less likely to use wetlands with extensive coverage of emergent vegetation (Murkin et al. 1997, Reynolds et al. 2006) and that blue-winged teal and mallard would be more likely to use wetlands with extensive emergent cover (Ringelman and Flake 1980, Bloom 2010).

Given our objective of learning about the potential utility of repeat-count surveys and hierarchical models for assessment of brood habitat, we were particularly interested in the relationships between ψ and characteristics of wetland basins and study plots. Wetland basins are the fundamental unit of habitat for breeding ducks in the PPR. The abundance of breeding pairs of dabbling ducks is positively related to the area of a wetland basin and pair density generally increases with basin perimeter, which is proportional to the logarithm of basin area (Cowardin et al. 1995, Reynolds et al. 2006).

We therefore modeled ψ relative to the logarithm of wetland area and predicted a positive relationship. Upland landscapes have the potential to affect reproductive success in dabbling ducks. Nest survival probability and survival of breeding females is positively related to the amount of perennial grass cover (or negatively related to the amount of cropland) in the landscape (Greenwood et al. 1995, Reynolds et al. 2001, Devries et al. 2003, Stephens et al. 2005). We predicted that ψ might thus be higher on plots with a greater proportion of perennial grass cover. We included two plot-level covariates describing the wetland conditions on each plot in each year as a potential way of indirectly controlling for variation in the size of the breeding pair population and the availability of wetland habitat for brood-rearing. We predicted that if the size of the pair population was positively related to the number of basins in May (Cowardin et al. 1995, Reynolds et al. 2006) then ψ would be positively related to the count of wet basins on the plot in May. Because female mallards, and presumably other ducks, select brood-rearing habitat non-randomly (Rotella and Ratti 1992, Raven et al. 2007, Bloom 2010), we predicted that ψ would be lower in landscapes with more available wetland habitat in July. That is, we thought that an individual basin's probability of occupancy by a brood might be lower given a greater amount of available, attractive wetland habitat during the brood-rearing period.

We predicted that given our somewhat limited and indirect knowledge of brood distribution, variation in ψ beyond that explained by the covariates was likely. We therefore included a plot-year-level distribution of random effects (i.e., a random effect for each plot in each year) in our model of ψ. These random effects provided additional

flexibility to control for missing covariates and potential overdispersion (Link and Barker 2009) and thus rendered our results more generally applicable to the population of 10.4-km^2 landscapes in the study area.

Our predictions about probability of detection were based on a relatively large group of past assessments of probability of detection of broods in the PPR. These surveys used diverse methods and were conducted on many different study areas during a roughly 30-year period, thus they provided a large body of information for constructing predictions about p. Wetland basins were the sampling unit in our study, thus we did not use brood-specific covariates in the analysis. We expected variation in p related to differences in brood-rearing behavior, brood age, and brood size to manifest as variation among species. In past multi-species studies, mallard and blue-winged teal broods had lower probability of detection than gadwall, pintail, or shoveler broods (Hammond 1970, Pagano and Arnold 2009). We expected p to be highest for gadwall because of their use of relatively open, semi-permanent wetlands (Murkin et al. 1997), and their likely larger average brood size in July (Klett et al. 1988). Further, we expected that older broods might be more detectable than younger broods (Ringelman and Flake 1980). Given that mallards and northern pintails nest earlier than other species, we expected mallard and pintail broods to be older than other broods and to therefore have higher p in our surveys.

To account for variation in p due to survey timing and habitat characteristics, we included several covariates in each species-specific model: date and time of the survey; wind speed during the survey; percent emergent vegetation cover and wet area of the surveyed basin; and a binary variable describing whether a brood had been observed on

that basin on the previous visit. We predicted that p would increase during the 15-day survey period if observers became more proficient or if broods became more detectable because of changes in age distribution (Ringelman and Flake 1980, Giudice 2001, Pagano and Arnold 2009). Broods are generally more active and thus more easily detected early and late in the day (Ringelman and Flake 1980, Pagano and Arnold 2009). Therefore, we modeled detection as a function of time of data using a quadratic curve, which we thought would be concave-up with the lowest detection probability associated with basin visits conducted during mid-day. Emergent vegetation obscures broods from view (Giudice 2001). Thus, we predicted that p would be negatively related to the area of the basin obscured by emergent vegetation. We predicted that p would be negatively related to wind speed if broods increasingly took cover in emergent vegetation or on shorelines as wind speed increased (Ringelman and Flake 1980, Giudice 2001, Pagano and Arnold 2009). We predicted that p would be negatively related to wet area surveyed because the observer's effectiveness might decrease with area (Pagano and Arnold 2009, A. Royle USGS, unpublished data). Other researchers have found strong evidence that p is higher on sampling units where the study organism was detected on a previous visit (Riddle et al. 2010), thus we predicted that detection probability would be higher when broods had been detected in a previous count.

Observer ability can affect p (Diefenbach et al. 2003, MacKenzie et al. 2006). Our surveys were conducted by a large group of observers whose identities varied among years. For the sake of efficiency, the same observer conducted all visits to a given plot in a given year. Thus, any observer effects were confounded with unspecified plot-year-

level variation that may have been present in p. We consequently used random-effects at the plot-year level (i.e., the data collected on a given plot in a given year) to account for variation in detection associated with variation in ability among observers and to account for variation in p among plot-years not captured by the covariates.

We obtained values of covariates for input to the model from three sources: 1) information recorded by observers; 2) geo-referenced, 1-m aerial videography of study plots (Cowardin et al. 1995, Reynolds et al. 2006); and 3) USFWS landcover maps (USFWS, unpublished data). Date (DATE), time (TIME), and wind speed (WIND) were recorded at each plot-visit. Percent of the surveyed basin area obscured by emergent cover (PCTEMRG) was recorded at each basin on the first visit. A binary covariate describing the expectation of detecting a brood, given a brood was detected at that basin on the previous visit (PRDET), was derived from the encounter history for each basin (MacKenzie et al. 2006, Riddle et al. 2010). Aerial videography of each surveyed plot was captured in May and July of each year and used to calculate wetland variables (Cowardin et al. 1995, Reynolds et al. 2006). Aerial videography was geo-referenced, wetland basins were digitized, and wet area was calculated with ArcView 9.3 (ESRI 2008). The wet area of each basin that intersected the 220-m survey buffer (WETAR) was used to characterize variability in surveyed basin area. The count of wetland basins containing water in May (MAYBASINS) was calculated from the May videography. The total area of wetland habitat on the plot during the survey (JULYWETAR) was derived by summing the area of digitized wetland basins on the plot in July. The

proportion of upland area on the plot composed of herbaceous perennial vegetation (PERCOV) was calculated from USFWS landcover (USFWS, unpublished data).

Our sampling design included a representative gradient of wetland basin size and plot-scale perennial cover, but it could not control for potential correlation among covariates due to changing wetland conditions among years. We consequently calculated summary statistics for observed covariates so that we could properly assess our inference space. Multicollinearity can cause difficulty with estimation of regression coefficients and sampling variances in statistical models (Graham 2003). We assessed potential multicollinearity by estimating pairwise correlations and Variance Inflation Factors (VIFs) using R (R Development Core Team 2010) and the *AED* package (Zuur et al. 2007). We removed any variables with VIF>3 from the analysis.

We used a version of the binomial mixture model developed and described by MacKenzie et al (2006) to estimate p and ψ given the observation and habitat covariates. The basic structure of this hierarchical, generalized linear mixed model was described by the following statements:

$$y_{ij} | z_i \sim \text{Bin}(\text{J}, z_i p_{ij})$$

$$\log\left(\frac{p_{ij}}{1\text{-}p_{ij}}\right) = \alpha_0 + \alpha_1 x_{ij1} + \ldots + \alpha_k x_{ijk} + ep_{\text{plot-year}}$$

$$z_i \sim \text{Bin}(1, \psi_i)$$

$$\log\left(\frac{\psi_i}{1-\psi_i}\right) = \beta_0 + \beta_1 x_{i1} + \ldots + \beta_k x_{ik} + epsi_{\text{plot-year}}$$

where y_{ij} was the observed presence of broods on basin $i = 1, 2,\ldots, I$ during visit $j = 1, 2,\ldots, J$, p_{ij} was the visit-level probability of detection, ψ_i was the basin-level probability of occupancy, the α_k and β_k were logit-scale regression coefficients associated with the predictors of detection and presence respectively, and the $ep_{\text{plot-year}}$ and $epsi_{\text{plot-year}}$ were plot-year-level random effects on detection and occupancy (Royle and Dorazio 2008). Random effects were modeled as normally distributed plot-year-level deviations from the overall mean (i.e., α_0 or β_0) with mean 0 and standard deviation $\sigma_{\text{plot-year}}$. The model was valid given the following critical assumptions: 1) the occupancy status of the basin remained constant during the survey, 2) variation in occupancy and detection among basins and visits was adequately described by the predictors and the random-effects, 3) detections of broods were independent among basins and visits, and 4) false-positive detections were rare or non-existent (MacKenzie et al. 2006; 104). We addressed the first assumption in two ways. At the basin level, we sought to minimize the potential effect of changes in occupancy status of wetlands by conducting all three visits in a 24-hour period. At the plot level, we incorporated the DATE covariate to account for a potential trend in ψ due to hatching and immigration of new broods and mortality and emigration of existing broods over the 15-day survey. We addressed the second and third assumptions by 1) using a group of covariates that were consistent with existing knowledge, 2) including the PRDET covariate to explicitly account for potential dependency in p among visits due to previous detections, 3) incorporating the more flexible random-effects structure, and 4) testing the model for lack-of-fit before making inferences. False positive detections of broods could have occurred if observers mistook

a group of fully-feathered adult ducks for a brood. However, we believe that such a mistake was rare because 1) broods can be distinguished from groups of adult ducks by plumage characteristics and behavior (Gollop and Marshall 1954) and 2) this potential violation of the fourth assumption was addressed in the sampling protocol and during observer training. Observers were instructed to carefully evaluate fully-feathered (i.e., class III) broods for bright plumage, a tendency to remain together, and flightlessness.

Our decision to use repeat-count surveys and a hierarchical, mixed-effects modeling approach helped to alleviate potentially serious problems associated with non-detection errors, missing covariates, and overdispersion but created a challenge for selecting a best-approximating model for inference. Hierarchical mixed-effects models are realistic and flexible, but they take much longer to program and run than their non-hierarchical counterparts. They also present significant, unresolved challenges for model selection (Gelman et al. 2004, Royle and Dorazio 2008, Link and Barker 2009). The number of covariates for ψ (6) and p (7) defined a large potential set of nested models for each species (i.e., $\geq 2^{13}$-2 models * 5 species), and we could not run these models in a reasonable amount of time. Given the a priori justification for the inclusion of each covariate, it was reasonable to believe that all combinations of covariates were plausible and to consider the set containing all possible combinations to be composed of well-justified models. Thus, no rationale was readily apparent for eliminating any covariate or group of covariates. However, our interest in making inference about covariate relationships required us to consider alternative models and to identify which model structures were supported by the data. Consequently, we took a two-stage approach to

the analysis. First, we used a maximum-likelihood approach to select a model, and then we estimated model parameters and random-effects distributions using Bayesian techniques (Royle and Dorazio 2008). We used the occupancy models in the contributed R (R Development Core Team 2010) package *unmarked* (Fiske and Chandler 2010) to select a reduced model by eliminating unsupported parameters (covariates) from the full, 15-parameter model for each of the five species. We used a "drop one" approach analogous to model reduction based on Type II sums-of-squares in ANOVA (Chambers 1992) to identify unsupported parameters. We removed a single parameter from the full model and estimated the AIC (Burnham and Anderson 2002) of the resulting reduced model. We then replaced that parameter and removed another parameter. We repeated this step for each of the parameters in the full model. This created a set of 13 models with either 13 or 14 parameters per model (a 13-parameter model was created when both TIME and $TIME^2$ were removed). We then examined the AIC difference between each reduced model and the full model. We defined unsupported parameters as parameters that were associated with a decrease in AIC relative to the full model when they were removed from the full model (i.e., removing these parameters increased model likelihood). We then removed the entire subset of unsupported parameters from the full model to create a reduced model for each species. Reduced models thus included the subset of parameters associated with increases in AIC relative to the full model when held out separately. Finally, we ran the resulting reduced model and compared its AIC value to the AIC value of the full model. We used the reduced model for inference when its AIC value was at least 2 units less than the AIC value of the full model. This strategy

allowed us to identify a more parsimonious subset of the parameters to use in mixed-effects models without running the entire set of potential candidate models.

In the second stage of analysis, we combined each of the five, species-specific subsets of the parameters selected in the first stage of analysis and used a simulation-based, Bayesian approach to obtain an estimate of the joint posterior distribution of the logit-scale coefficients and standard deviations of the random effects distributions. We chose minimally informative, compact prior distributions for model parameters (Royle and Dorazio 2008). Logit-transformed uniform (0, 1) prior distributions were used for intercept terms. Uniform (-10, 10) prior distributions were used for logit-scale slope coefficients. Uniform (0, 10) prior distributions were used for the standard deviations of random-effects distributions. To assist convergence, values of each covariate were standardized by subtracting the mean and dividing by the standard deviation of the observed values prior to use in analysis. TIME was squared after standardization and log(WETAR) was standardized after taking the log.

Using the R (R Development Core Team 2010) package *R2WinBugs* (Sturtz et al. 2005) as an interface to WinBUGS 1.4 (Spiegelhalter et al. 2003), we ran 2 Markov chains for each model with 200,000 simulations for each chain and discarded the first 100,000 simulations as burn-in. We evaluated convergence to the posterior distribution by inspection of plots of consecutive simulation draws for each chain and by the Gelman-Rubin statistic (R-hat; Gelman et al. 2004). We used a posterior predictive test to address potential lack-of-fit between the model and the data. Specifically, we tested for lack-of-fit by comparing the value of a Chi-squared-type discrepancy statistic calculated from the

observed data to the value of the same statistic calculated from replicated data at each simulation draw (Kèry and Royle 2010; also see WinBUGS code in Appendix 1). Under the hypothesis that the mixed-effects hierarchical occupancy model was not an inappropriate model for the data, the proportion of draws where fit of the replicated data exceeded the fit of the observed data was expected to fall between 0.01 and 0.99 (Gelman et al. 2004). As a measure of the number of effectively uncorrelated samples obtained from the joint posterior, we calculated the effective sample size (ESS; Kass et al. 1998, Streftaris and Worton 2008) with built-in functions in the contributed R package *CODA* (Plummer et al. 2009).

To make inference about ψ and p, we combined the 100,000 post-burn-in simulations from each chain and used them to construct posterior distributions of logit-scale regression coefficients, standard deviations of random effects distributions, and back-transformed estimates of occupancy and detection probability at selected covariate values. We evaluated the relationships between ψ (or p) and the covariates based on the magnitude and direction of estimated coefficients, the number of species showing a similar pattern, and the medians and 90% credible intervals (90% CIs) of the estimated posterior distributions of logit-scale regression coefficients and back-transformed probabilities. To evaluate the magnitude of covariate effects, we varied a single covariate while holding other variables constant at their mean values and evaluated 1) absolute change in probability and 2) probability ratios. When the same coefficient was included in models for multiple species and 90% credible intervals did not include zero, we presented results for the 2 species with the smallest and largest response to the covariate.

Results

Our sample comprised 167 plots and 3,226 wetland basins. We sampled 77 plots in 2007, 146 plots in 2008, and 148 plots in 2009: 26 plots were surveyed in a single year, 78 plots were surveyed in 2 of the three years and 63 plots were surveyed in all three years. We conducted 4,356 basin-level surveys during the study: 2,213 basins were surveyed in a single year, 896 basins were surveyed in two of the three years, and 117 basins were surveyed in all three years. Each basin was visited 3 times, thus the data consisted of 3 * 4,356 = 13,068 basin visits. Variation in the number of sample plots and basins resulted from expansion of the survey and from variation in wetland conditions caused by variability in precipitation.

The percent of basins where at least 1 brood was detected in at least 1 visit varied among species and was generally less than 15% (Fig. 2). Blue-winged teal were detected in approximately 12%, mallard in 9%, gadwall in 8%, northern shoveler in 5% and northern pintail in 3% of the 4,356 basin-level surveys. Consistent with species-specific breeding chronology, the median age class (Gollop and Marshall 1954) of detected blue-winged teal (22 days–33 days), mallard (26 days–35 days), northern pintail (34 days–43 days), and northern shoveler (28 days–35 days) broods was greater than the median age of detected gadwall broods (15 days–18 days). Size of detected broods was similar among species. A median brood size of 5 ducklings was observed for detected broods of blue-winged teal, mallard, northern pintail, and northern shoveler. Median size of detected gadwall broods was 6 ducklings.

Covariate conditions were consistent with our goal of sampling a gradient of wetland basin area and perennial cover, and correlations among covariates were not large enough to hamper estimation or interpretation. We observed a wide range of survey conditions, wetland area, and landscape characteristics (Table 1). Wet area of sampled basins ranged from 0.003 ha to 106.350 ha. The proportion of perennial cover ranged from 0.03 to 0.99 on sample plots. Correlations among detection predictors ranged from -0.15 to 0.29 and VIFs ranged from 1.00 to 1.10. Correlations among occupancy predictors ranged from -0.33 to 0.20 and VIFs ranged from 1.01 to 1.13. The set of basin-level mean covariate conditions used to calculate derived estimates of p and ψ described a 2.7-ha wetland basin with about 40% coverage of emergent vegetation surveyed at approximately 1300 hours on 25 July at a wind speed of 7 kmph–19 kmph. Mean landscape-level covariates described a 10.4-square-km area with 53% of the upland composed of perennial grass cover, 64 wetland basins containing water in May, and about 77 ha of wetland habitat in July (Table 1).

Maximum-likelihood model selection confirmed that reduced models were more parsimonious than the full model for four of the five species. For blue-winged teal, mallard, northern pintail, and northern shoveler, the reduced model represented a substantial reduction in AIC relative to the full model. The full model was within 2 AIC units of the reduced model for gadwall (Table 2). Reduced occupancy-detection models ranged in complexity from 10 parameters for mallard to 14 parameters for gadwall. The occupancy part of the model contained from 4 to 7 parameters depending on species. DATE was retained in the reduced occupancy model for every species but blue-winged

teal. PCTEMERG was retained in the reduced occupancy model for gadwall, northern pintail, and northern shoveler. MAYBASINS was retained in the reduced occupancy model for blue-winged teal, gadwall, and mallard. PERCOV was retained in the reduced occupancy model for every species except mallard. JULYWETAR was retained in the reduced occupancy model for gadwall, mallard, northern pintail, and northern shoveler. Log(WETAR) was retained in the reduced occupancy model for all five species. The detection part of the model contained from 5 to 7 parameters depending on species. DATE was retained in the reduced detection model for gadwall and northern pintail. TIME and $TIME^2$ were retained in the reduced detection model for blue-winged teal, northern pintail, and northern shoveler. TIME was retained in the reduced models for gadwall and mallard. WIND was retained in the reduced detection model for blue-winged teal and gadwall. EMERG was retained in the reduced detection model for blue-winged teal, gadwall, and mallard. PRDET was retained in the reduced detection model for every species but northern pintail. WETAR was retained in the reduced detection model for every species.

The second-stage Bayesian analysis provided useful estimates of structural parameters for each species-specific, reduced model. The hierarchical mixed-effects occupancy model converged to the posterior distribution of all fixed-effects coefficients and random-effects standard deviations for every species. R-hat values were < 1.1 for all parameters. The lack-of-fit test provided no evidence of model failure. All posterior proportions were near the center of the 0.01, 0.99 interval. The proportion of simulations where the discrepancy between the model and simulated data exceeded the discrepancy

between the model and the observed data was 0.47, 0.43, 0.48, 0.45, and 0.46 for blue-winged teal, gadwall, mallard, northern pintail, and northern shoveler respectively. Model runs were time-intensive as expected. Up to 500 simulations were required to produce an effectively uncorrelated draw from the joint posterior for some species–parameter combinations. All structural parameters nonetheless had ESS >150 per chain and most had ESS>500 per chain. Depending on the species, 200,000 simulations took approximately 50 hours-75 hours on a desktop computer with an 8-core by 2.26 GHz processor and 12 GB of RAM.

Observed variation in probability of occupancy among species and with survey date was largely consistent with predictions (Fig. 3). Given mean observed values of the covariates, posterior median $\hat{\psi}$ (lower 90% CI, upper 90% CI) was 0.33 (0.30, 0.38), 0.24 (0.20, 0.28), 0.16 (0.13, 0.19), 0.12 (0.09, 0.15), and 0.10 (0.06, 0.14) for blue-winged teal, mallard, gadwall, northern shoveler, and northern pintail, respectively. The probability of occupancy of wetlands by gadwall, mallard, northern pintail, and northern shoveler decreased during the 15-day survey period. DATE was not included in the reduced model for blue-winged teal. Occupancy by northern pintail decreased from 0.14 (0.09, 0.20) to 0.04 (0.01, 0.09) during the survey, and occupancy by mallard declined from 0.29 (0.24, 0.35) to 0.14 (0.10, 0.20).

Consistent with our predictions, occupancy of wetlands by broods was positively related to the area of individual wetlands, positively related to the proportion of perennial grass cover on the 10.4-km^2 study plots, and negatively related to the amount of the basin covered by emergent vegetation for most species. Observed relationships between

wetland occupancy by broods and landscape-level wetland conditions were less consistent with our predictions (Fig. 4). We observed a positive relationship between $\hat{\psi}$ and log(WETAR) for every species. As WETAR increased from 0.19 ha to 2.12 ha (inter-quartile range; Table 1), the median probability of a wetland basin being occupied by a gadwall brood more than tripled from 0.08 (0.07, 0.10) to 0.28 (0.24, 0.33). Over the same range of WETAR, $\hat{\psi}$ of blue-winged teal broods increased by a factor of 1.76 (1.59, 1.96) from 0.25 (0.21, 0.29) to 0.44 (0.39, 0.49). Gadwall, northern pintail, and northern shoveler broods were less likely to occupy wetlands with greater coverage of emergent vegetation; PCTEMRG was not included in reduced models for mallard and blue-winged teal. Compared to wetland basins that were completely obscured by emergent vegetation, basins with no emergent vegetation were nearly 3 times more likely to be occupied by gadwall broods (range of $\hat{\psi}$ from 0.23 [0.19, 0.29] to 0.08 [0.06, 0.12]) and 4 times more likely to be occupied by northern pintail broods (range of $\hat{\psi}$ from 0.16 [0.10, 0.23] to 0.04 [0.02, 0.07]). PERCOV was associated with increases in $\hat{\psi}$ for all species but mallard. As the proportion of perennial grass cover on a 10.4-km^2 study plot increased from 0.03 to 0.99, probability of basin occupancy by a blue-winged teal brood increased by a factor of 1.49 (1.12, 1.99) from 0.27 (0.21, 0.33) to 0.40 (0.34, 0.47) and probability of occupancy by a northern pintail brood increased by a factor of 3.72 (2.15, 6.64) from 0.05 (0.03, 0.08) to 0.18 (0.11, 0.26). Coefficients describing relationships of $\hat{\psi}$ to plot-level, wetland covariates (JULYWETAR and MAYBASINS) were negative when they were included in reduced models and their 90% credible intervals did not

overlap zero. As JULYWETAR increased from 0.13 ha to 406.35 ha, probability of occupancy by gadwall decreased from 0.12 (0.07, 0.17) to 0.04 (0.02, 0.09) and probability of occupancy by northern pintail decreased from 0.13 (0.08, 0.20) to 0.02 (0.01, 0.06). Probability of occupancy by blue-winged teal and mallard decreased from 0.37 (0.32, 0.42) to 0.17 (0.08, 0.34) and 0.32 (0.27, 0.38) to 0.03 (0.01, 0.07), respectively, as MAYBASINS increased from 1 to 442.

As predicted, there was substantial unexplained variation in occupancy for all five species. The logit-scale standard deviation of the plot-year random-effects for $\hat{\psi}$ was 0.84 (0.66, 1.04), 0.79 (0.57, 1.00), 0.85 (0.65, 1.05), 0.56 (0.10, 1.04), and 1.10 (0.87, 1.37) for blue-winged teal, gadwall, mallard, northern pintail, and northern shoveler, respectively. For northern pintail, the species with the smallest standard deviation, median probability of occupancy with all covariates held constant at their mean values ranged from 0.03 (0.01, 0.10) to 0.24 (0.14, 0.39) over a range of $2\,\hat{\sigma}_{epsi_{plot-year}}$. For northern shoveler, the species with the largest standard deviation, median probability of occupancy with all covariates held constant at their mean values ranged from 0.01 (0.01, 0.03) to 0.55 (0.44, 0.67) over a range of $2\,\hat{\sigma}_{epsi_{plot-year}}$.

Median probability of detection was generally less than 0.3 and was clearly lower for northern pintail than the other 4 species. At mean covariate values, the median (lower 90% CI, upper 90% CI) of the estimated posterior distribution of detection probability ($\hat{p}$) was 0.27 (0.27, 0.31) for blue-winged teal, 0.29 (0.24, 0.36) for gadwall, 0.27 (0.23,

0.31) for mallard, 0.12 (0.07, 0.20) for northern pintail, and 0.23 (0.18, 0.29) for northern shoveler.

Reduced models of probability of detection relative to covariates describing survey timing and conditions differed among species as did estimated coefficients and credible intervals (Fig. 5). A coefficient for DATE was included in reduced models for gadwall and northern pintail. At the median of the posterior distribution, the relationship between DATE and probability of detection was positive for both species, but 90% credible intervals overlapped zero. Reduced models for four of the five study species included negative coefficients for TIME and positive coefficients for $TIME^2$. Credible intervals for both coefficients overlapped zero for gadwall and northern pintail. The credible interval for the $TIME^2$ coefficient overlapped zero for mallard. Probability of detection for blue-winged teal and northern shoveler was highest early and late in the day as predicted. Probability of detection of blue-winged teal broods decreased by 27% (17%, 35%) from 0.37 (0.32, 0.43) to 0.27 (0.23, 0.31) between 0600 hours and 1100 hours and then increased 13% (0%, 33%) to 0.31 (0.24, 0.40) between 1100 hours and 2000 hours. Probability of detection of northern shoveler broods decreased from 0.35 (0.27, 0.44) to 0.23 (0.18, 0.29) between 0600 hours and 1100 hours and increased again to 0.28 (0.17, 0.42) between 1100 hours and 2000 hours. Probability of detection of mallard broods decreased linearly throughout the day from 0.34 (0.28, 0.39) to 0.18 (0.14, 0.23). Windy conditions were associated with reduced median probability of detection of blue-winged teal and gadwall. This variable was not included in reduced models for other species. When WIND increased from calm conditions to Beaufort level

6 (about 45 kilometers per hour), $\hat{p}$ of blue-winged teal decreased from 0.30 (0.25, 0.36) to 0.21 (0.16, 0.26), and $\hat{p}$ of gadwall decreased from 0.36 (0.28, 0.44) to 0.20 (0.14, 0.28). Reduced models for four of the five species indicated that detection was substantially more likely when a brood was detected during the previous visit. Previous detection (PRDET) was not included in the model for northern pintail. PRDET was associated with a 42% (24%, 66%) increase in $\hat{p}$ of mallard from 0.27 (0.23, 0.31) to 0.38 (0.34, 0.43) and a 48% (28%, 67%) increase in $\hat{p}$ of blue-winged teal from 0.27 (0.23, 0.31) to 0.40 (0.36, 0.45).

Consistent with our predictions about relationships between probability of detection and wetland characteristics, $\hat{p}$ varied with wetland area and the percent of the wetland covered by emergent vegetation. Broods of all 5 species were more difficult-to-detect on large wetlands (Fig. 5). When WETAR increased from 1 ha to 20 ha, $\hat{p}$ of northern pintail declined from 0.14 (0.8, 0.23) to 0.08 (0.05, 0.14), and $\hat{p}$ of mallard declined from 0.28 (0.24, 0.32) to 0.25 (0.21, 0.29). Broods of blue-winged teal, gadwall, and mallard were less frequently detected on wetlands with higher PCTEMERG. When PCTEMERG increased from 0% to 100%, $\hat{p}$ of gadwall decreased from 0.36 (0.28, 0.43) to 0.21 (0.13, 0.32), and $\hat{p}$ of mallard decreased from 0.40 (0.34, 0.46) to 0.13 (0.10, 0.16).

Our prediction about unexplained variation in $\hat{p}$ among plot-years was supported. Estimated, logit-scale, median standard deviations of random-effects distributions (i.e., $\hat{\sigma}_{ep_{plot-year}}$) were 0.78 (0.62, 0.93), 1.07 (0.84, 1.31), 0.65 (0.45, 0.85),

1.17 (0.77, 1.55), and 0.81 (0.58, 1.06) for blue-winged teal, gadwall, mallard, northern pintail and northern shoveler, respectively. This variation was substantial. For mallard, the species with the smallest standard deviation, median detection probability with all covariates held constant at their mean values ranged from 0.08 (0.09, 0.11) to 0.57 (0.52, 0.62) over a range of $2\hat{\sigma}_{ep_{plot-year}}$. For northern pintail, the species with the largest standard deviation, median detection probability with all covariates held constant at their mean values ranged from 0.01 (0.00, 0.05) to 0.58 (0.47, 0.70) over a range of $2\hat{\sigma}_{ep_{plot-year}}$.

Discussion

Our research was built on a foundation of past studies of brood ecology and brood surveys and took advantage of recent developments in occupancy sampling and modeling to develop a new understanding of the late-summer distribution of duck broods across the PPR relative to habitat covariates. The repeat-count, wetland based survey approach that we used was applied effectively by a diverse group of field workers across a large study region. The hierarchical, mixed-effects occupancy model that we applied to our extensive, repeat-visit brood survey sample converged to the posterior distribution of all structural parameters, displayed no evidence of lack-of-fit, and provided posterior estimates of model parameters that were interpretable in the context of existing knowledge of brood ecology and probability of detection. This combination provided a useful and informative tool for identifying wetland basins and landscapes associated with higher probability of occupancy by broods across the PPR.

We observed clear relationships between occupancy of wetlands by broods and habitat characteristics at the scale of both wetland basins and landscapes. These relationships were informative in the context of current knowledge of duck ecology in the PPR. In keeping with our predictions, probability of occupancy increased with the log of wetland area for all five species. This basin-level association was the strongest and most consistent relationship that we observed between occupancy of wetlands by broods and habitat characteristics. This pattern is consistent with the repeatedly observed pattern of use of larger seasonal and semi-permanent wetlands by broods (Talent et al. 1982, Rotella and Ratti 1992, Krapu et al. 2006, Raven et al. 2007, Bloom 2010). The number of breeding pairs of the study species occupying a wetland also tends to increase with wetland area at a decreasing rate (Cowardin et al. 1995). This pattern is thought to result from a non-linear increase in the availability of productive shallow-water habitat associated with increasing wetland area (Reynolds et al. 2006). It was also notable that we found evidence that landscape-scale features were related to occupancy for most species. In particular, we observed substantial increases in probability of occupancy as the amount of perennial grass cover on a site increased. For example, the estimated rate of wetland occupancy for northern pintail increased from 1 brood per 20 basins (13, 39) to 1 brood per 6 basins (4, 9) as perennial cover increased from 3% to 99%. There were multiple, non-mutually exclusive explanations for this pattern. It might have been that our prediction that reproductive success is higher in landscapes with greater amounts of perennial vegetation was correct. Higher nest survival of the study species has been repeatedly observed in landscapes with greater amounts of perennial cover (Greenwood

et al. 1995, Reynolds et al. 2001, Stephens et al. 2005). Duckling survival of the study species is related to weather events and landscape-level wetland conditions and appears to be less affected by upland landscape characteristics like proportion of perennial cover (Krapu et al. 2000, Pietz et al. 2003), but there is some evidence that interactions between upland composition and wetland communities can be associated with higher duckling survival (Bloom 2010). An alternative explanation for the relationship between probability of occupancy and perennial cover is that wetland basins in less intensively cultivated landscapes might provide higher-quality food resources (Gleason et al. 2003) leading to greater pair densities on sites with greater amounts of perennial cover (Reynolds et al. 2006). Such a relationship could also result if less wetland habitat were available on sites with more perennial cover such that any broods produced had fewer choices of which wetlands to use, but this was unlikely the case for our data ($r = 0.018$ between the number of wet basins on a plot in May and perennial cover and $r = -0.008$ between total wet area on a plot in July and perennial cover). In contrast to the other species, probability of occupancy was not associated with perennial cover for mallard broods. This pattern might be related to the distribution of mallard pairs in the study region. Breeding mallards tend to be more widespread than some other common duck species in the PPR, occupying wetlands in landscapes with low levels of perennial cover at about the same density as wetlands in high perennial cover landscapes (Cowardin et al. 1995, Reynolds et al. 2006).

The probability of detecting a brood was low and variable in our study. This result was consistent with our predictions and the results of past investigations

(Ringelman and Flake 1980, Giudice 2001, Pagano and Arnold 2009). These results imply that investigations of the distribution and abundance of duck broods should account for detection probability in order to provide useful information. Probability of detection in brood surveys simply cannot be ignored or made constant by elaborate operating procedures (Pagano and Arnold 2009). In our study, standardization of the operating procedure to maximize mean detection probability and minimize variation in detection among basin-visits would have required sampling small wetland basins of identical area with no emergent vegetation early in the morning on a single day. This severely restricted target population would not have been as informative as the larger population we were able to sample with repeated-counts. Our results further highlighted the utility of a hierarchical modeling approach that allowed simultaneous assessment of population state and detection probability relative to covariates. Both detection probability and probability of occupancy were related to wetland area, survey date, and emergent cover. Any modeling approach that did not separate these variables would therefore have resulted in parameter estimates that were difficult or impossible to interpret in an ecological context (Royle and Dorazio 2008). Our results indicated that, at a minimum, brood surveys need to consist of two visits to each sample unit to provide reliable information. Given that median detection probability was less that 0.5 for most species, 3-5 visits to each sample unit would be preferable and might even be necessary under more refined objectives. For example, at a median detection probability of 0.25, 6 visits would be required to discriminate occupied from unoccupied wetlands with probability 0.80 at the level of a single species. Interest in multiple species, occupancy

states, or more informative state variables like abundance would lead to more intensive sampling requirements both in terms of the number of sites (in this case wetland basins) and the number of visits (MacKenzie et al. 2006).

Despite its ability to provide an informative description of the likely distribution of broods at a regional extent, our survey could not identify separately the effects of pair abundance, habitat use, and reproductive success on probability of wetland occupancy by broods. For example, similar rates of wetland occupancy by broods could be observed in landscapes where high densities of breeding pairs had modest levels of reproductive success as in landscapes where lower densities of breeding pairs had high reproductive success. Nor could our approach provide a direct inventory of the number of broods. Our results indicated that these more detailed objectives would require more intensive count surveys; detailed studies of individually marked breeding females, nests, and broods; or a combination of both approaches. For example, early and late surveys of breeding pairs followed by early and late surveys of broods (Cowardin and Blohm 1992, Cowardin et al. 1995, Pagano and Arnold 2009) could provide estimates of brood abundance and brood to pair ratios at the landscape level that would be comparable among species. Regardless of intensity, extensive count surveys cannot match the detail and potential for increase in basic knowledge provided by studies of individually marked animals. We therefore regard these approaches as complementary. For example, information gathered from extensive count surveys might be used both to inform conservation and management programs and to direct and design more detailed studies of marked individuals.

Much remains to be learned about habitat relationships of dabbling ducks from patterns of occupancy of wetland basins by broods in late summer across the PPR. Spatial and temporal variation in environmental conditions produces substantial variation in settling patterns of ducks and reproductive success. This variation occurs on multiple spatial and temporal scales. We suggest that the continuation of this extensive brood survey, with modifications to the sampling design to better account for the breeding chronology of different species, would be a useful way to learn about spatial and temporal variation in brood distribution relative to changes in wetland conditions and ecosystem productivity. These changes are substantial and are associated with cycles of wetness and drought at more extensive time-scales than captured by our study. A longer-term approach would be useful for learning about which wetland basins and landscapes were consistently associated with higher levels of occupancy by broods. An inventory of the number of consistently occupied basins in a given landscape would be useful for managers seeking to identify important landscapes for ducks and generate hypotheses for more intensive studies of habitat relationships.

Management Implications

Management of breeding waterfowl in the PPR is largely focused on the identification and conservation of wetland and upland habitat where both abundance of breeding pairs and reproductive success are high. Current targeting of habitat conservation in this region is largely guided by knowledge of the distribution and relative abundance of breeding pairs (Reynolds et al. 2006) and knowledge of variation in nest survival probability (Reynolds et al. 2001, Stephens et al. 2005). Managers and

researchers have long recognized an additional need for interpretable measures of habitat that can be collected rapidly across a large extent and used to identify wetland basins and landscapes that provide important brood habitat. Using a repeat-count survey design and a hierarchical mixed-effects modeling approach, we developed an informative model of distribution of duck broods of the five most common breeding duck species in the PPR relative to landscape and wetland characteristics that are important for management. Our model could be applied to the problem of identifying wetland basins and landscapes that are consistently more likely to be occupied by broods, providing a basis for evaluation of alternative conservation actions based on the amount of potential brood habitat in a given landscape. There is also potential for repeat-visit survey designs to provide new information based on recent developments in hierarchical modeling of data from count surveys (Royle and Dorazio 2008). Additional data collected under our sampling design could be used in a multi-state occupancy context to develop a temporally explicit picture of basins that are likely to be occupied by broods over multiple years and to identify landscapes with the greatest number of these basins. Multi-species occupancy models could be used with data like ours to identify wetland basins that are more likely to be occupied by multiple species, assuming a more-intensive sampling design that was tuned to target these basins. Applications like these could provide flexible, new tools for habitat evaluation and assessment under multiple objectives.

Waterfowl habitat in the PPR is largely in private ownership and is continentally important for both migratory bird populations and agricultural production. Habitat conservation efforts for breeding waterfowl in the PPR are focused on perpetual

conservation of grassland and wetland habitat given limited budgets. Our brood survey approach represents a viable alternative to single visit pair surveys for identifying landscapes that provide important habitat for breeding waterfowl and could be used to increase the effectiveness and efficiency of conservation planning in a region like the PPR.

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Table 2.1 Descriptive statistics for observed covariates used in a hierarchical occupancy model describing variation in the distribution of duck broods in North and South Dakota, USA during 2007-2009.

Probability	Covariate[a]	Level	Min.	Q1	Med.	Q3	Max.	Mean	SD
Detection (p)	TIME	Count	360	487	664	852	1213	685.89	213.43
	WIND	Count	0	1	2	3	6	2.19	1.19
Occupancy (ψ)	JULYWETAR	Plot	0.13	33.73	61.96	107.82	406.35	76.58	61.62
	MAYBASINS	Plot	1.00	27.00	45.00	72.00	442.00	64.22	65.24
	PERCOV	Plot	0.03	0.23	0.54	0.82	0.99	0.53	0.29
Both (p and ψ)	PCTEMRG	Basin	0	10	30	80	100	40	34
	WETAR (ha)	Basin	0.00	0.19	0.63	2.12	106.35	2.68	7.58
	DATE	Plot	1	2	6	8	17	5.87	4.04

[a]Definitions of covariate names: TIME was the time in minutes since 12 am CDT that the count took place, WIND was the wind level during the visit according to the ordinal Beaufort scale, JULYWETAR was the summed hectares of wetland area on the 10.4-km^2 study site in July, MAYBASINS was the count of wetland basins holding water on the 10.4-km^2 study plot in May, PERCOV was the proportion of the upland area of the10.4-km^2 study plot composed of perennial vegetation, PCTEMRG was the proportion of the surveyed basin covered by emergent vegetation, WETAR was the number of hectares of wet area associated with the surveyed basin, and DATE was the date the survey was conducted (day 1 = July 20).

Table 2.2 Models of occupancy and detection of duck broods reduced by using changes in AIC to identify and remove parameters that made little contribution to fit of the full model. Differences in AIC between the full and reduced models (i.e., AIC_{full}-$AIC_{reduced}$) were 5.7, 1.2, 8.2, 4.7, and 7.1 for blue-winged teal (BWTE), gadwall (GADW), mallard (MALL), northern pintail (NOPI), and northern shoveler (NSHO) respectively. Covariate abbreviations are defined in Table 2.1.

Occupancy Model						
Species	DATE	EMERG	PERCOV	MAYBASINS	JULYWET	log(WETAR)
BWTE	0[a]	0	1	1	0	1
GADW	1	1	1	1	1	1
MALL	1	0	0	1	1	1
NOPI	1	1	1	0	1	1
NSHO	1	1	1	0	1	1

Detection Model							
Species	DATE	TIME	$TIME^2$	WIND	EMERG	PRDET	WETAR
BWTE	0	1	1	1	1	1	1
GADW	1	1	0	1	1	1	1
MALL	0	1	0	0	1	1	1
NOPI	1	1	1	0	0	0	1
NSHO	0	1	1	0	0	1	1

[a]A 1 indicates that the parameter in each column was included in the reduced model, and a 0 indicates that it was not included.

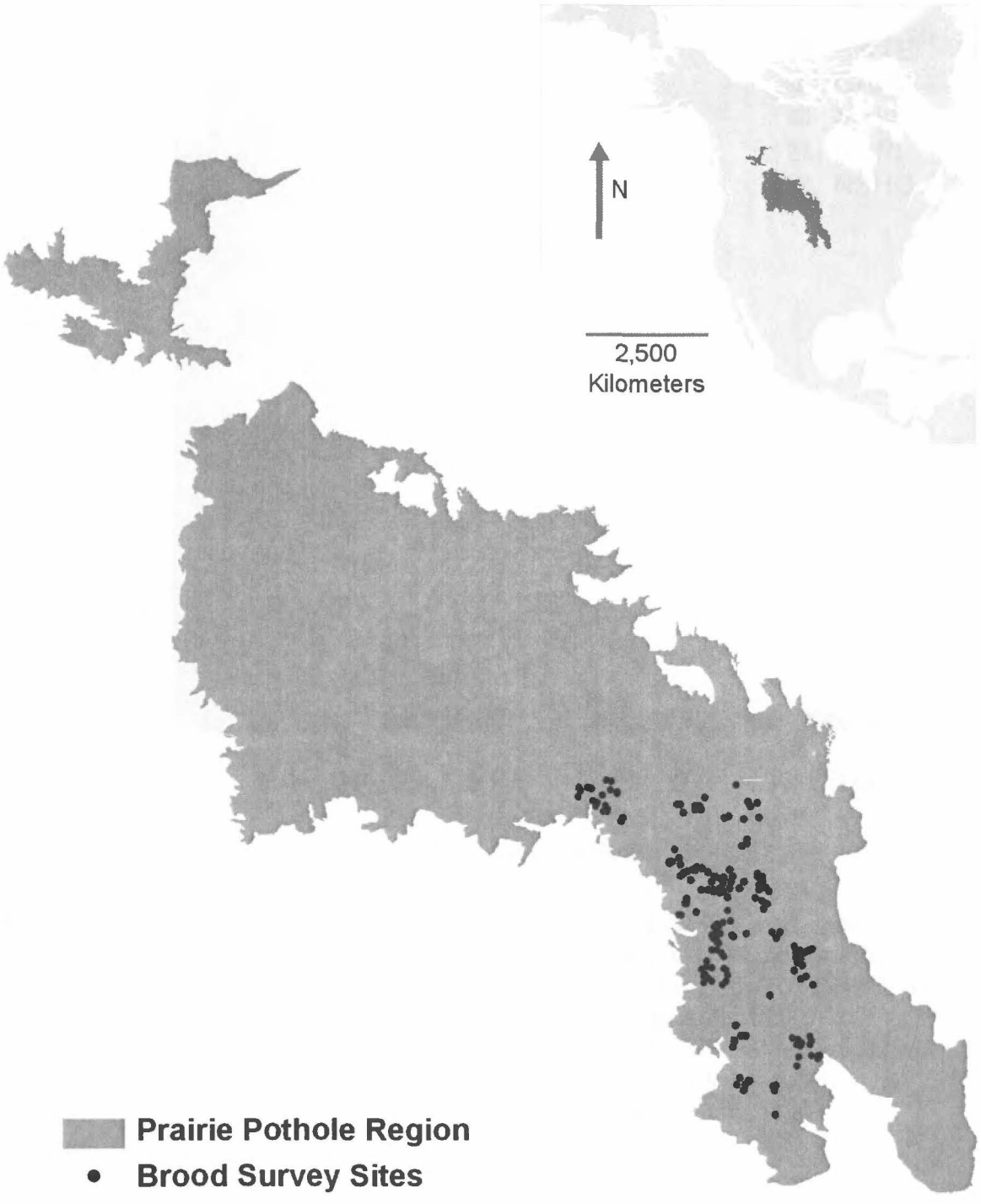

Figure 2.1 Location of plots and extent of the study area used for surveys of duck broods in the Prairie Pothole Region during late summer 2007-2009.

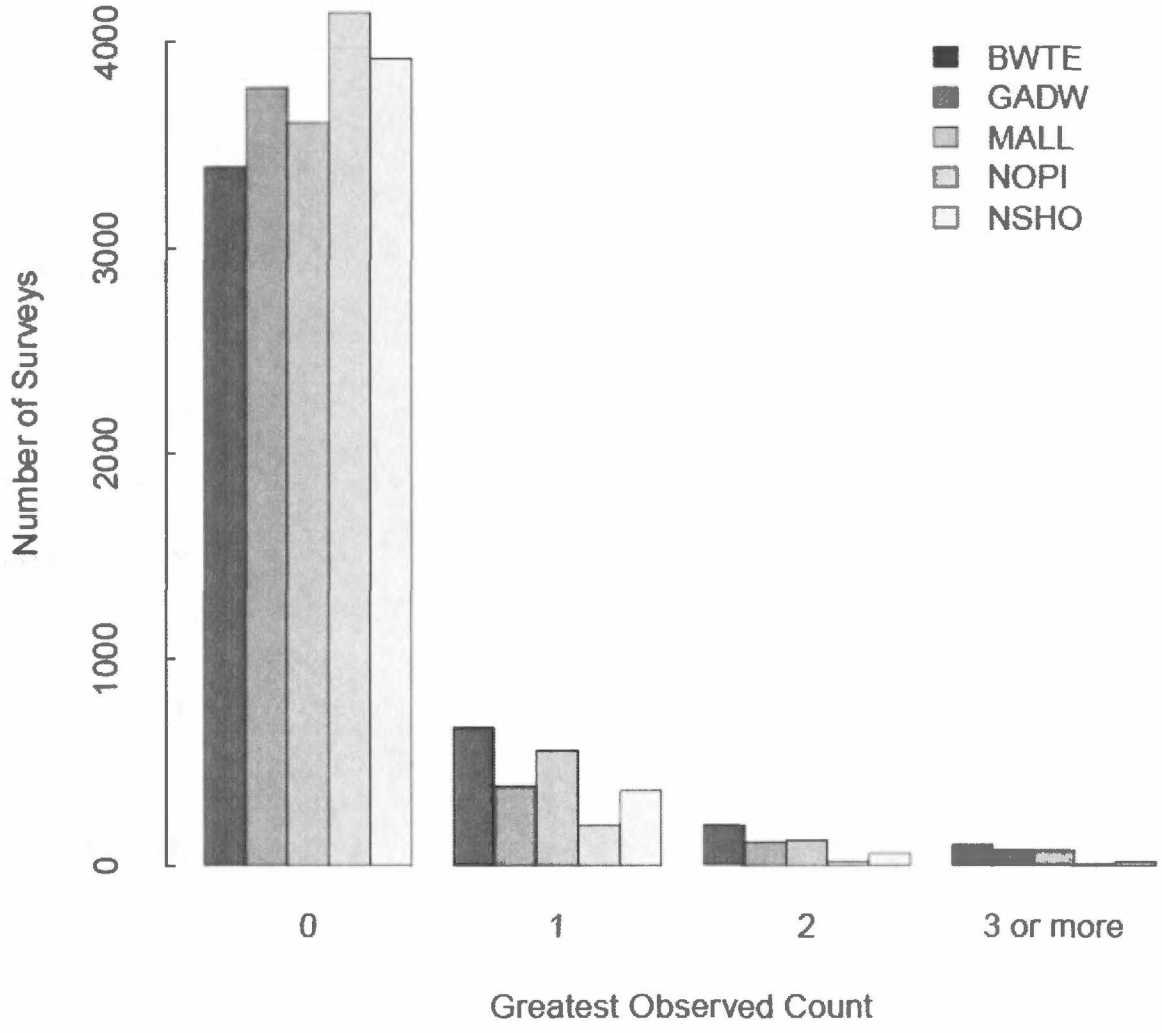

Figure 2.2 Summary of the maximum number of broods of the five most common breeding duck species (blue-winged teal [BWTE], gadwall [GADW], mallard [MALL], northern pintail [NOPI], and northern shoveler [NSHO]) that were detected in a 3-visit survey of wetland basins conducted during late July and early August 2007-2009 in North and South Dakota USA. Zero broods were detected on 78% to 95%, and one or fewer broods were detected on 93% to 99% of the 4,356 basin-level surveys.

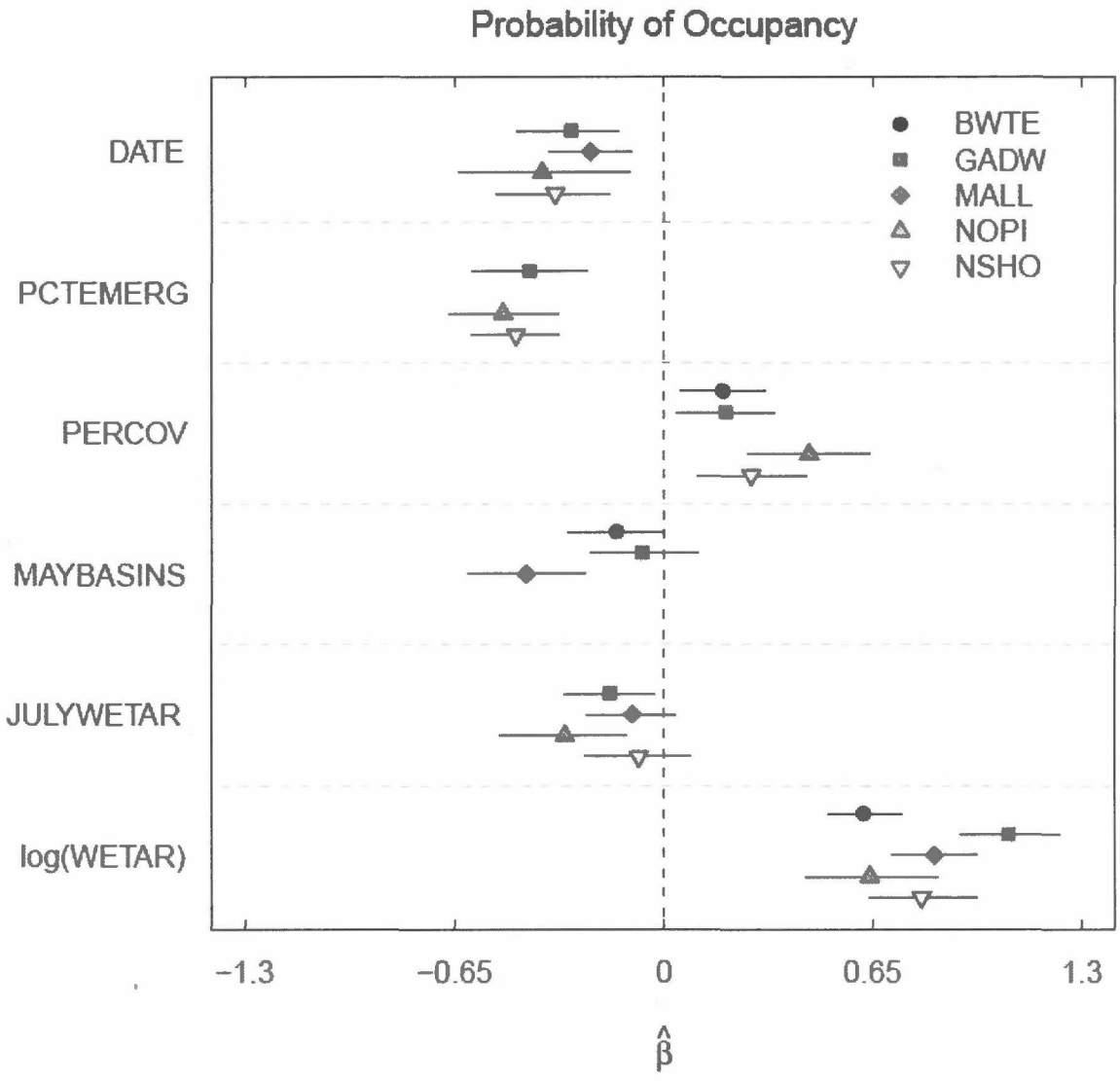

Figure 2.3 Logit-scale occupancy coefficients ($\hat{\beta}$) taken from species-specific hierarchical models of occupancy of wetland basins by duck broods relative to date of the survey (DATE), the percent of the surveyed wetland area covered by emergent vegetation (PCTEMERG), the natural logarithm of wet basin area log(WETAR), the proportion of the upland area of 10.4-km^2 study plot covered by perennial grassland (PERCOV), the number of wetland basins containing water on the 10.4-km^2 study plot (MAYBASINS), and the total area of wetlands on the 10.4-km^2 study plot during the survey (JULYWET). Points are estimated posterior medians. Horizontal lines represent 90% of the estimated posterior density of each parameter.

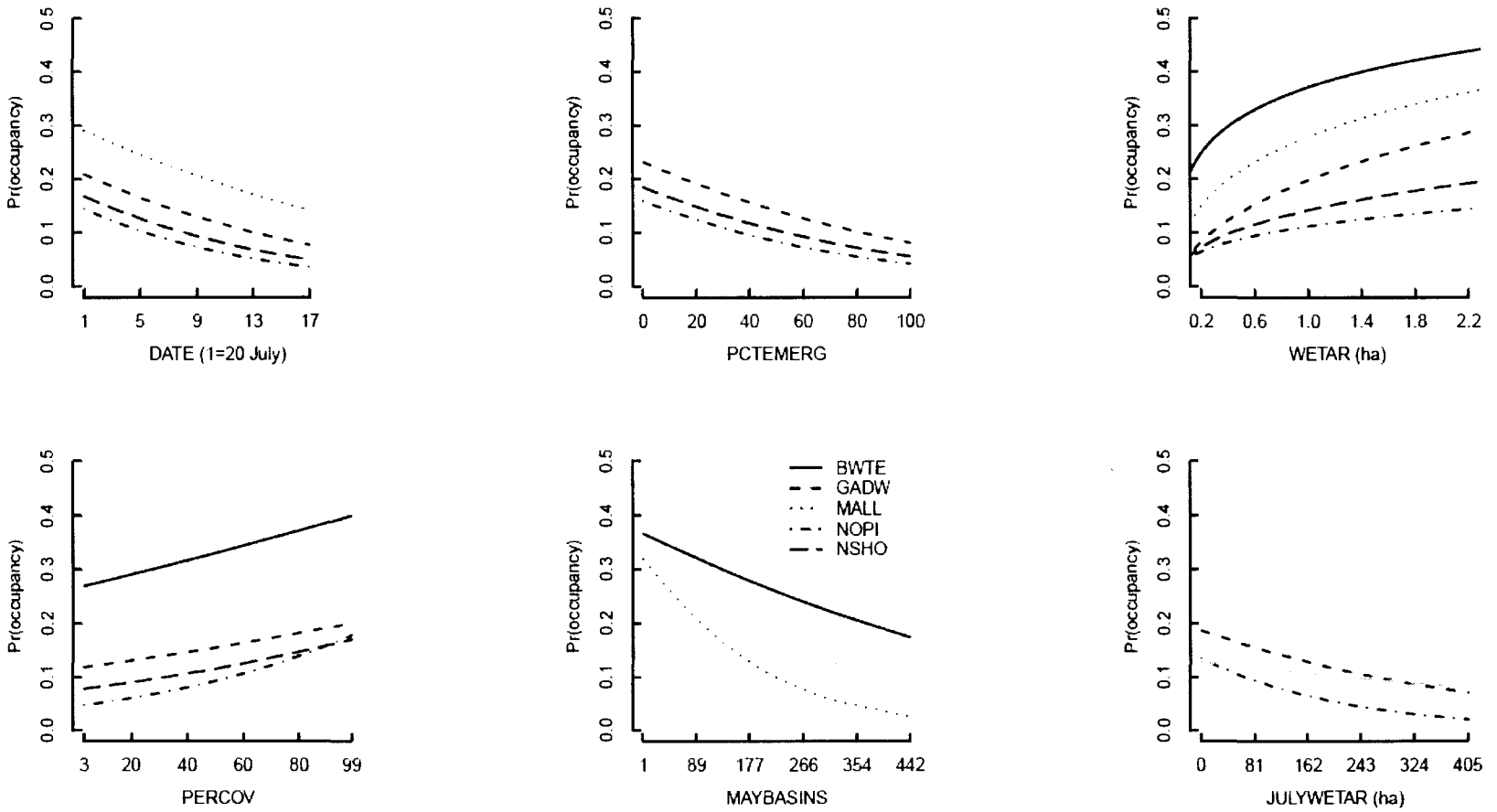

Figure 2.4 Predicted median probability of wetland occupancy by duck broods during late-summer relative to habitat covariates. Relationships were calculated with other covariates in the model held constant at their mean values. Light gray lines indicate 90% credible intervals that overlapped zero. Covariate abbreviations are defined in Table 2.1.

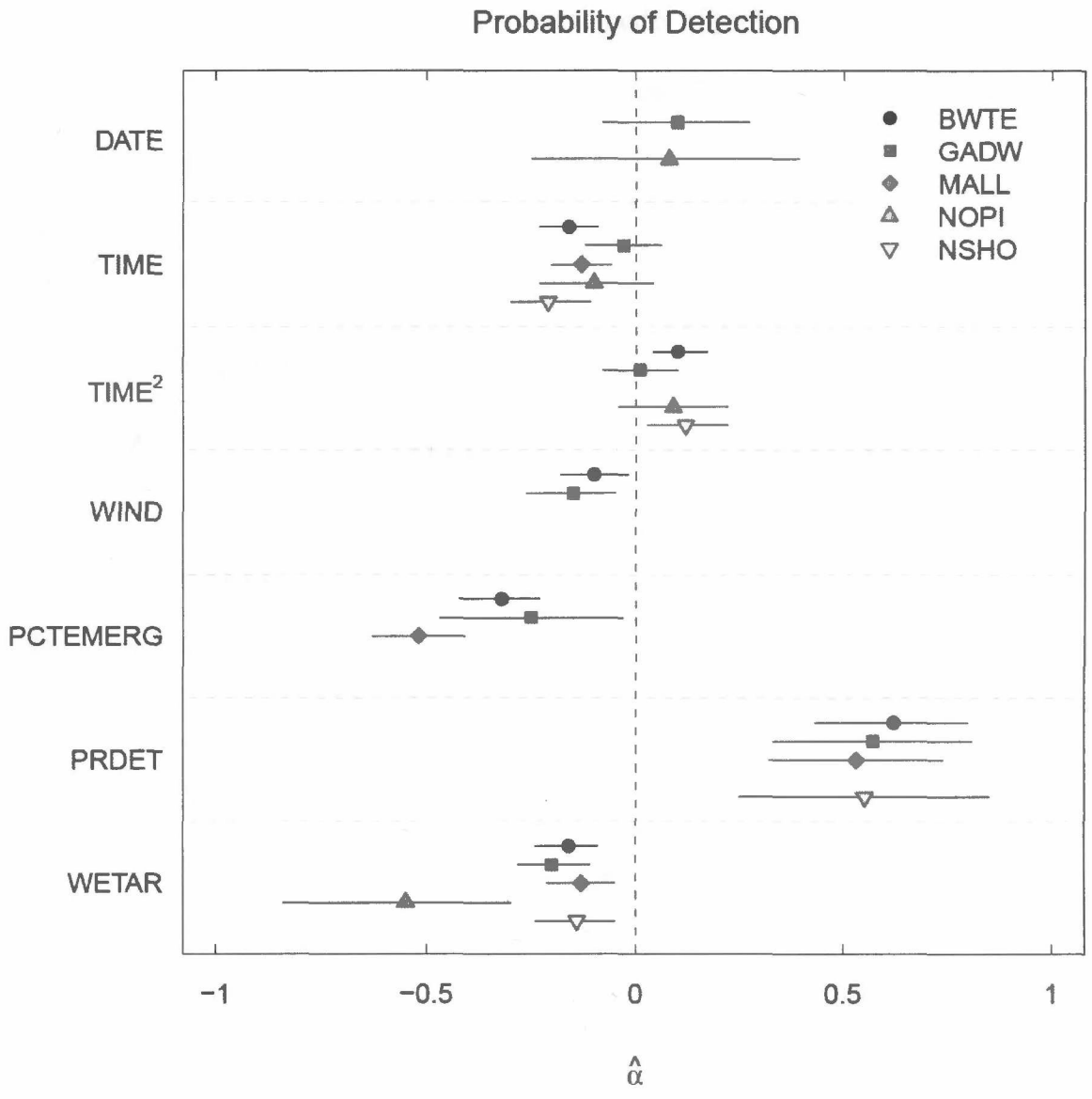

Figure 2.5 Logit-scale detection coefficients ($\hat{\alpha}$) taken from species-specific hierarchical models of occupancy of wetland basins by duck broods relative to date (DATE) and time (TIME) of the survey, the wind speed during the survey (WIND), the percent of the surveyed wetland area covered by emergent vegetation (PCTEMERG), whether a brood had been detected on a previous visit (PRDET), and the amount of wet area surveyed (WETAR). Points are estimated posterior medians. Horizontal lines represent 90% of the estimated posterior density of each parameter.

Appendix 1: WinBUGS code for a hierarchical model of probability of wetland occupancy and probability of detection of duck broods. This code was modified from Royle and Dorazio (2008) and Kèry and Royle (2010).

```
# Occupancy Priors
psi0 ~ dunif(0,1)
b0 <- log(psi0/(1-psi0))
for (k in 1:6) {
b[k] ~ dunif(-10,10)}
sigmapsi ~ dunif(0,10)
taupsi <- pow(sigmapsi,-2)
for (k in 1:nplotyears) {
epsi[k] ~ dnorm(b0, taupsi)}
# Detection Priors
p0 ~  dunif(0,1)
a0 <- log(p0/(1-p0))
for (k in 1:7){
a[k] ~ dunif(-10,10)}
sigmap ~ dunif(0,10)
taup <- pow(sigmap,-2)
for (k in 1:nplotyears) {
ep[k] ~ dnorm(a0, taup)}
```

```
# Occupancy Likelihood
for (i in 1:nbasins) {
 Z[i] ~ dbin(psi1[i], 1)
 etapsi[i] <- b[1]*date[i]+ b[2]*pctemerg[i] + b[3]*percov[i] +
b[4]*maybasins[i] + b[5]*julywetar[i] + b[6]*logwetar[i] +
epsi[plotyear[i]]
 psi[i] <- 1 / (1 + exp(-etapsi[i]))
 psi1[i]<- min(0.999999,max(0.000001,psi[i]))}
# Detection Likelihood
for (j in 1:nvisits) {
 eta[j] <- a[1]*date[j] + a[2]*time[j] + a[3]*timesquared[j] +
   a[4]*wind[j] + a[5]*pctemerg[j] + a[6]*prdet[j] +
   a[7]*wetar[j] + ep[plotyear[j]]
 p[j] <- 1 / (1 + exp(-eta[j]))
p1[j]<- min(0.999999,max(0.000001,p[j]))
muy[j] <- Z[plot[j]]*p1[j]
y[j] ~ dbin(muy[j], 1)
y.rep[j] ~ dbin(muy[j], 1)}
```

```
# Discrepancy statistic and Bayesian p-value for assessing lack-of-fit
for (j in 1:nvisits) {
E[j] <- pow((y[j]-muy[j]),2)/(muy[j]+0.5)
E.new[j] <- pow((y.rep[j]-muy[j]),2)/(muy[j]+0.5)
}
fit.obs <- sum(E[])
fit.new <- sum(E.new[])
pval <- step(fit.new-fit.obs)
```

Chapter 3. Integrated targeting of conservation easement acquisition for waterfowl increases conservation benefits in the Prairie Pothole Region[1]

Abstract

Limited budgets and increasing rates of habitat loss ensure that efficiency is a critical consideration for conservation planning. Benefit-based conservation plans based on targeting rules that direct funding to areas with the highest ecological benefit without considering risk of habitat loss or cost of protection can be inefficient. We evaluated the need for and opportunity to refine current, benefit-based targeting strategies for the acquisition of perpetual conservation easements on privately owned grasslands in the Prairie Pothole Region of North and South Dakota, and we proposed a path toward integrated targeting of future acquisitions. Need was apparent from the negative trend in the area protected each year and the large observed increases in easement cost (248%) and landowner-reported cropland rental rate (40%) during 2000–2009. Opportunity was apparent in comparisons of protected and unprotected area. The straightforward, benefit-based targeting scheme used in the past had been very effective: 89% of the area protected during 2000–2009 was located in priority landscapes with greater than 10 breeding duck pairs/km^2. Current protected area

[1] Prepared for submission to *Human-Wildlife Interactions* as Walker, J., A. Smith, J. J. Rotella, C.M. Hunter, R. W. Renner, J. K. Ringelman, S. E. Stephens, M. S. Lindberg, and C. R. Loesch. Toward integrated targeting of grassland easement acquisition for waterfowl habitat conservation in the Prairie Pothole Region.

differed from unprotected area in terms of its potential risk of conversion to cropland and cost of protection. The observed proportion of protected land with relatively low suitability for cultivation (i.e., at low risk of conversion) was greater than the observed proportion of unprotected grassland with relatively low suitability for cultivation. There was a statistically significant difference between the distribution of protected and unprotected grassland with respect to the quartiles of potential cost of protection, but the observed proportion of land above and below the median cost was the same for both groups. Of the 58,881 km^2 of remaining unprotected grassland habitat, 15,938 km^2 was located in landscapes identified as the highest conservation priority under the current system. This area was nearly 6 times larger than the 2,792 km^2 protected during 2000–2009 and was heterogeneous in terms of risk of conversion and cost of protection. We proposed a refined targeting scheme that refocused protection efforts on the 3,189 km^2 of unprotected highest-benefit habitat composed of greater than 75% high-risk grassland and located in counties with cost index values below the 25th percentile. Assuming 2009 easement costs and budgets, we conducted a hypothetical exercise to determine the potential gain in conservation value from the refined approach and concluded that focusing on this smaller area would potentially lead to a 24% decrease in easement cost per hectare and a 20% increase in the amount of protected area. Adoption of this new prioritization and an adaptive approach to monitoring progress and checking assumptions would help to counter increasing demand for cropland and protect more critical habitat in our study area.

Key-words: Agricultural Landscapes, Conservation Planning, Cost of Protection, Ecological Benefit, Habitat Loss, Migratory Birds, Private Land Conservation,

The ratio of converted to protected land in many of the Earth's major biomes and ecoregions exceeds 8:1 (Hoekstra et al. 2005). Both acute and chronic habitat losses are ongoing worldwide (Laurance 2010). Budgets for conservation are limited (Underwood et al. 2008), and, as a result, the question of how best to allocate funds to specific conservation actions has received considerable recent attention (Pressey et al. 2007, Arthur et al. 2008). Conservation planners have long used predictions from spatially explicit models of relationships between ecological parameters and habitat characteristics to rank and prioritize alternative sites (Margules and Pressey 2000). The simplicity and directness of a benefit-based strategy is appealing, but more comprehensive strategies are often warranted. Conservation planning based solely on ecological benefits can be inadequate when budgets are limited and the risk of habitat loss and cost of protection also vary among sites (Newburn et al. 2005, Naidoo et al. 2006, Underwood et al. 2008).

The primary objective of most conservation planning is to develop a strategy to protect as much of the existing ecological benefit as possible (Margules and Pressey 2000, Pressey et al. 2007). In landscapes where ecological benefit, risk of habitat loss, and cost of protection vary among sites, a benefit-only conservation strategy can often be improved by additional information. Heterogeneity in risk and

cost can create opportunity to protect a greater amount of ecological benefit with a given budget: for example, by discriminating against sites with low expected benefit per unit cost (Wilson et al. 2005, Naidoo et al. 2006, Drechsler et al. 2007). In landscapes where ecological benefit occurs mostly on privately-owned lands and is continually diminished by changing land use practices, integrated approaches to conservation planning can provide a way to maximize effectiveness of habitat protection efforts (Newburn et al. 2005, Naidoo and Iwamura 2007).

Privately owned lands provide important wildlife habitat in agricultural landscapes (Drechsler et al. 2007, Naidoo and Iwamura 2007), and the value of habitat for wildlife in agricultural landscapes is often negatively related to intensity of land use (Claassen 2001, Foley et al. 2005). Land use intensification, particularly conversion of native vegetation to annually cultivated cropland, is an important mechanism of benefit loss in these landscapes (Laurance 2010). Conversion to cultivated from uncultivated uses also results in increased land prices (Xu et al. 1993, Carriazo et al. 2009) creating economic inertia that can work against conservation and future restoration of habitat. An increasingly used and effective tactic for conserving ecological benefits on privately owned agricultural lands is thus to purchase, in perpetuity, the right to cultivate (Fishburn et al. 2009, Enck and Cojocariu 2010, Murdoch et al. 2010). Perpetual conservation easements can provide cost-effective protection of ecological benefit while allowing participating landowners to continue to realize economic benefit from a restricted set of less-intensive land use options such as livestock grazing or forage production.

Agricultural landscapes tend to exhibit variation in ecological benefit, risk of conversion, and cost of protection (Reynolds et al. 2006, Naidoo and Iwamura 2007, Stephens et al. 2008, Enck and Cojocariu 2010, Rashford et al. 2010). As a result, the most effective conservation plans for targeting easement acquisition programs in these landscapes are likely those that make explicit trade-offs among these components. Motivated by recent trends in habitat loss and land values, we set out to use existing information to explore the need and opportunity to develop an integrated strategy for prioritizing easement acquisitions on private agricultural lands in the north central United States.

We evaluated conservation easement acquisition in the Prairie Pothole Region (PPR) of North and South Dakota, USA (Fig. 1). Billions of dollars have been expended to protect and restore grassland and wetland habitat in the PPR for the benefit of migratory bird populations (United States Fish and Wildlife Service and Canadian Wildlife Service 1986, Skagen and Thompson 2001, Kushlan 2002, Ringelman 2005). Much of the conservation funding spent in this region has been used to purchase conservation easements that protect ecological benefits for migratory birds through perpetually prohibiting cultivation of privately owned grasslands and wetlands. The United States Fish and Wildlife Service (USFWS) conservation easement program is a substantial conservation effort that has allocated about $10,000,000 annually to the perpetual protection of grassland habitat during the past 10 years (USFWS, unpublished data). To date, this program has been targeted solely based on ecological benefit, although both rate of habitat loss (Stephens et al.

2008, Rashford et al. 2010) and land value (United States Department of Agriculture, National Agricultural Statistics Service 2011) are variable across the region. During the past decade, increased loss rates of grassland (Stubbs 2007, Stephens et al. 2008), increased commodity prices, and increased cropland values (United States Department of Agriculture, National Agricultural Statistics Service 2011) have been documented across the PPR. These recent trends indicated that the need for more efficient targeting of easement acquisition might also have increased.

We had three specific objectives for our assessment of easement acquisition strategy in the PPR of North and South Dakota (hereafter, PPR): 1) to assess need for refined targeting by examining recent trends in habitat protection, protection cost, and cropland value; 2) to assess opportunity for refined targeting by comparing the extent, ecological benefit, risk of conversion to cropland, and cost of protection of perpetually protected habitat and remaining unprotected grasslands; and 3) to evaluate the potential benefit of a refined prioritization strategy for easement acquisitions that incorporated information about of risk of conversion and land value in addition to ecological benefit.

Methods

Our study area (Fig. 1) was part of a globally important region both for agriculture and migratory birds. Most land in the PPR is privately owned and used for production of small grains, row-crops, or livestock (Johnson et al. 1994). North and South Dakota are major producers of wheat (*Triticum aestivum*) and cattle (*Bos taurus*), and recently these states have shown increases in planted area of corn (*Zea*

mays) and soybeans (*Glycine max*; United States Department of Agriculture, National Agricultural Statistics Service 2011). The native, mixed-grass prairie and shallow wetlands of the PPR provide critical breeding habitat for large populations of wetland- and grassland-dependent migratory birds (United States Fish and Wildlife Service and Canadian Wildlife Service 1986, Skagen and Thompson 2001, Kushlan 2002, Ringelman 2005). This area is particularly important for populations of waterfowl (*Anatidae*). It has the highest density of palustrine wetland basins and breeding ducks in the United States (Reynolds et al. 2006, Zimpfer et al. 2009). Loss of wetland and grassland habitat to cultivation is thought to cause population declines of grassland-dependent species through changes in population dynamics brought about through changes in predator communities and ecosystem function (Sargeant et al. 1993, Samson and Knopf 1996). Northern pintails have declined concurrently with agricultural intensification of their primary breeding areas in the PPR (Miller and Duncan 1999). Grassland songbird populations in the PPR have also shown large declines in abundance, which are thought to be related to land use (Peterjohn 2003, Brennan and Kuvlesky 2005). Effectively protecting grassland and wetland habitat through perpetual conservation easements is thus an important component of contemporary conservation efforts in the PPR.

We were interested in using existing information and working within the current system of easement targeting to assess the need and opportunity for a more integrated strategy. We thought that our approach would reveal strengths and weaknesses of both the current strategy and the available information and provide for

straightforward implementation of a refined strategy if warranted. We assessed need for refined targeting by 1) evaluating the trends in prices paid for easements and area of easements acquired during 2000–2009 and 2) comparing these trends to a) available information about cropland value across the region and b) to projected losses of grassland based on the results of recent research. We assessed opportunity for refined targeting by comparing recently acquired easements with remaining unprotected habitat in terms of benefit, risk of conversion, and cost of protection. (We defined opportunity as the combination of 1) the existence of substantial area of currently unprotected habitat of high ecological benefit, at high risk of loss, and low cost of protection and 2) evidence of successful targeting under the current system). We used ArcGIS (ESRI 2008) for mapping and analysis of spatial data, and we used R 2.1.0 (R Development Core Team 2010) to generate summary statistics, estimate parameters of statistical models, and perform statistical tests.

We used easement acquisition data from the USFWS (USFWS, Bismarck, ND, Unpublished Data), the results of recent research on grassland conversion (Stephens et al. 2008, Rashford et al. 2010), and information about recent trends in the value of cropland (United States Department of Agriculture, National Agricultural Statistics Service, North Dakota Office 2011, United States Department of Agriculture, National Agricultural Statistics Service, South Dakota Office 2011) to assess the need for refined targeting of easement acquisition. We predicted that the amount of habitat protected had recently declined, that land value and easement costs had recently increased, and that protection activity had declined to a point where even

in an unlikely scenario with perfect targeting of at-risk habitat and no displacement of conversion current protection effort was unlikely to offset projected losses. We used linear regression (Neter et al. 1996) and the USFWS data to test for a negative trend in the amount of habitat protected during 2000–2009. We compared recent protection activity to projected cumulative and mean annual losses using a compound-interest model (Bronshtein et al. 2007): that is, $A_t = A_0(1+r)^t$ where A represented remaining grassland area, t represented time, and r represented the mean annual loss rate. We parameterized the model with the area of unprotected grassland at the start of 2009 as the initial condition, and iterated the model for 10 time steps with annual loss rates of 0.5%, 1.0%, and 1.5%. The loss rates we used encompassed the range of estimates presented by Rashford et al. (2010) for the study area. We calculated cumulative loss as the difference in area between the first and last time step and mean annual loss as the arithmetic mean of the time-step-level differences in area. We used data from an annual USDA survey of cropland rental rate in each of the counties in the study area to generate an average rental rate for each year. We compared average annual rental rate to the amount paid by USFWS for the easement area acquired each year. We calculated the average annual easement cost per area by dividing the total area of easements acquired by the total number of dollars paid for easements in each year. All dollar amounts were standardized to 2009 using the GDP implicit price deflator. Finally, to test for correspondence between cropland rental rate and easement cost, we estimated the linear correlation between these variables.

We assessed opportunity for refined easement targeting by comparing the distribution of grassland habitat protected during 2000–2009 with the distribution of remaining unprotected grassland in terms of ecological benefit, risk of conversion, and cost of protection. We had two general predictions for this analysis given past targeting efforts: 1) we predicted that most of the protected area would fall within the highest priority areas as defined by the FSMS pair density layer given active targeting of easements to these categories, and 2) we predicted that all grasslands should have proportionally similar distributions for conversion risk and land value regardless of protection status given that there had been little or no active targeting of easements to these components.

We used several publicly available GIS layers and ArcGIS (ESRI 2008) to characterize both recently acquired easements and remaining unprotected grasslands according to ecological benefit, risk of conversion, and cost of protection. We used three unpublished GIS layers that were available from the USFWS Habitat and Population Evaluation Team (HAPET) office in Bismarck, ND. The first was a polygon layer that showed extent and location of all grassland and wetland easements held by the USFWS. This layer also included a year attribute, which allowed us to select and characterize the easements acquired during our study period. The second was a USFWS landcover classification developed from Landsat Thematic Mapper (TM) satellite imagery to that we used to identify unprotected grassland habitat. We defined unprotected grasslands as pixels classified as grassland and undisturbed grassland in the USFWS landcover that did not intersect existing grassland easements

or lands owned by conservation agencies. To maintain consistency and coherence of our calculations at the scale of the region, we standardized the area of protected and unprotected grasslands to the regional baseline using the proportion of pixels in the USFWS landcover that were classified as either grassland or undisturbed grassland as weights (Nusser and Goebel 1997). Third, we used the USFWS Four-Square-Mile Survey (FSMS) breeding pairs layer to characterize landscapes according to ecological benefit. We acquired data pertaining to conversion risk and cost of protection from the United States Department of Agriculture (USDA). To address conversion risk, we used data from the USDA National Resource Conservation Service (NRCS) Soil Survey Geographic database (SSURGO; Natural Resources Conservation Service 1995). To address cost of protection, we used average county-level cropland rental rate derived from an annual USDA survey of landowners in each county across the study area (United States Department of Agriculture, National Agricultural Statistics Service, North Dakota Office 2011, United States Department of Agriculture, National Agricultural Statistics Service, South Dakota Office 2011).

We used the FSMS pairs layer to calculate the USFWS index of ecological benefit for each existing grassland easement and for the remaining unprotected grasslands. The pairs layer contained model-based estimates of the expected number of breeding pairs of the most common and abundant species of breeding ducks in the region for each 2.59-km^2 Public Lands Survey Section (PLSS) grid cell in the study area (Cowardin et al. 1995, Reynolds et al. 2006). The FSMS pair density index is widely used to prioritize grassland and wetland easement acquisitions. Under the

current benefit-based targeting strategy, priority is given to easements located in areas where expected pair density is predicted to be greatest. Highest priority is given to easements located in areas with greater than 23 pairs/km^2, and progressively lower priority is given to landscapes with 16 pairs/km^2–23 pairs/km^2 and 10 pairs/km^2–15 pairs/km^2. Landscapes with fewer than 10 pairs/km^2 are avoided. This prioritization is applied under the assumptions that this index of long-term density of breeding duck pairs is sufficient to describe habitat value for ducks, and that habitat states that are associated with a higher density of breeding duck pairs are favorable for many other species of migratory birds (Ringelman 2005, Reynolds et al. 2006, Quamen 2007).

Because we were unaware of any existing process to classify grassland habitat by its risk of conversion to cropland, we developed an index of conversion risk based on publicly available soils data. The probability of conversion of grassland to cropland is positively related to its suitability for crop production (Stephens et al. 2008, Rashford et al. 2010). We used Land Capability Class (LCC) values from the SSURGO database to develop an index of the risk of conversion. LCC is an ordinal variable that ranges from 1 to 8 that increases with increasing limitations to cultivation (Natural Resources Conservation Service 1995). We calculated the percent area of existing grasslands composed of LCCs 1, 2, 3, and 4, which are the classes that are widely regarded as most suitable for cultivation and are most vulnerable to conversion (Dosskey et al. 2006, Rashford et al. 2010). We intersected the PLSS grid with the digital SSURGO data for North and South Dakota and calculated the percent area of each 2.59 km^2 grid cell composed of LCC<5. The

conversion risk index thus had the same resolution as the pair density index (2.59 km^2) and ranged from 0 to 100.

We used reported, county-level cropland rental rates during 2000–2009 as an index to variation in cropland values, and thus easement cost, across the study area (United States Department of Agriculture, National Agricultural Statistics Service, North Dakota Office 2011, United States Department of Agriculture, National Agricultural Statistics Service, South Dakota Office 2011). In developing a cost of protection index from these data, we assumed that rental rate paid for cropland would be proportional to cropland value, which we expected to be proportional to the cost of easement acquisition (Xu et al. 1993, Naidoo et al. 2006). Our cost index had much coarser spatial resolution than the pair density or conversion risk index, but county-level rental rates during the recent period represented the only readily available information describing spatial variation in land value across the study area (Naidoo et al. 2006). There had been no past targeting of easement acquisition based on cost of protection, so we were interested in finding out whether this index of cost was informative.

To compare protected and unprotected grasslands in terms of pair density, conversion risk and protection cost, we categorized protected and unprotected grasslands and tested for differences between distributions using a Chi-squared goodness-of-fit test (Sokal and Rohlf 1995). In each of the three cases, we tested the null hypothesis that the proportional area in each category did not differ between protected and unprotected areas against the alternative hypothesis that the

proportional area differed in at least 1 category. We expected the proportion of protected area to be heavily weighted toward landscapes with pair index values greater than 10 given the current targeting strategy. Thus we predicted that the proportional area with pair index values greater than 10 would be greater in the protected than unprotected sample with the bulk of the protected area in landscapes with pair density index values greater than 23. There had been no active targeting on conversion risk or protection cost, thus we suspected that the proportional area of protected and unprotected habitat to be similar with respect to these indices. As a consequence of the active targeting for pair density, we chose to compare distributions of conversion risk and protection cost in areas where pair density values were greater than 10. We categorized the distribution of conversion risk in these areas according to the following scale: 0-25, 26-50, 51-75, 76-100 corresponding to the percent area of the landscape composed of LCC<5, and we categorized the distribution of protection cost according to its empirical quartiles. We considered chi-squared statistics that had a probability of 0.05 or smaller under the null hypothesis of identical distributions to be statistically significant, and we conducted all statistical tests in R 2.10.0 (R Development Core Team 2010). We considered differences to have practical significance for conservation when they led to different conclusions about the opportunity for refined targeting. For example, if the targeted area based on benefit was also composed of grassland at high risk of conversion and was located in landscapes with relatively low cost of protection, and the unprotected area was

similarly distributed, then we would conclude that there was little opportunity for refined targeting.

We used the results of the comparison of currently protected and unprotected grasslands to define categories for alternative targeting and prioritizations for grassland protection. We focused attention on the unprotected grassland habitat that was located in landscapes with pair density index values greater than 23 and made comparisons of alternative scenarios in the context of the current capacity for protection. We estimated the area of unprotected grassland in priority categories of high pair density, high conversion risk, and low cost of protection, and used these to evaluate the potential for refined easement acquisition strategies. We examined the distribution of unprotected habitat working from the category that is defined as highest priority under the current strategy (pair density>23) to subsets with higher conversion risk and lower cost-of-protection to determine whether the capacity for protection (relative to the acquisition level over the past 10 years) existed for each subset.

To further assess the potential for integrated targeting to improve effectiveness of current protection efforts, we evaluated the potential gains from refocusing easement acquisition efforts on the highest-benefit, highest-risk, lowest-cost unprotected habitat. As an approximation to the current targeting strategy, we randomly sampled from a subpopulation of 2.59-km^2 sections of high conservation value (i.e., pair index value greater than 23 and at least 0.65 km^2 of unprotected habitat classified as grassland or undisturbed grassland) and we evaluated the

potential area conserved with the typical recent annual budget. Then, we compared the area conserved by randomly sampling from a more-targeted subset with risk index values greater than 75 and easement cost below the 25th percentile. To translate rental rates to easement cost, we multiplied the cost index of unprotected lands by the observed ratio of per hectare easement cost to per hectare cropland rental rate in 2009. We then compared overall protection cost per hectare and total potential area of breeding habitat protected for both hypothetical scenarios.

Results

We calculated that 65,460 km^2 were classified as grassland or undisturbed grassland in the USFWS landcover as of 2009. An area of approximately 5,100 km^2, about 8% of total grassland area, had been protected by perpetual grassland easements at that time. About 55% of the total easement area (2,792 km^2) was acquired during 2000–2009. The greatest acquisition in a single year was 418 km^2 in 2000. The least was 195 km^2 in 2003. The median annual acquisition was about 257 km^2. Total expenditures (in 2009 dollars) were $98,840,011. Minimum annual expenditure was $5,953,160 in 2003. Median annual expenditure was $10,300,000. Maximum was $13,095,386 in 2008. Another 4,549 km^2 of protected area was held in fee-title by Federal and state conservation agencies. After subtracting the area of protected grassland from total grassland area, 58,811 km^2 of unprotected grassland remained in the study area. The majority (60%) of the unprotected grassland, an area of about 33,051 km^2, was located in landscapes with pair index values greater than 10.

Patterns of recent easement acquisition were consistent with our predictions. The trend in annual easement acquisition during 2000–2009 was negative ($F_{1,8}$ = 6.07, p = 0.04, R^2 = 0.43). The estimated mean additional area protected in 2000 was 349 km^2 (95% Confidence Interval [CI]: 272 km^2 to 425 km^2) and decreased by an estimated 15 km^2 (95% CI: 1 km^2 to 30 km^2) annually (Fig. 2). In 2009, estimated mean protected area was 210 km^2 (95% CI: 133 km^2 to 287 km^2). Comparison of annual protection activity with projected annual losses of grassland showed that projected losses exceeded recent protection at all but the lowest loss rates examined (Fig. 2). Given an initial area of 33,051 km^2 and constant loss rates of 0.5%, 1.0%, and 1.5%, projected average annual losses were 193 km^2, 316 km^2, and 463 km^2. Projected cumulative losses were thus 1,930 km^2, 3,160 km^2, and 4,636 km^2, respectively. Easement cost and cropland rental rate increased sharply (Fig. 2), and these variables were strongly correlated during the period (r = 0.97; 95% CI: 0.89 to 0.99). Average easement cost per hectare increased by approximately 248% from \$210 to \$730 while average cropland rental rate per hectare increased by approximately 40% from \$114 to \$161.

The results of our comparison of the distributions of protected and unprotected grassland were not entirely consistent with our predictions, although patterns in the data appeared consistent with our over-arching hypothesis that there was opportunity for refined targeting. As we predicted, benefit-based targeting of easements had concentrated the distribution of protected area in targeted landscapes (Table 1), and we rejected the null hypothesis that protected area and remaining

unprotected grasslands were distributed equivalently among the 4 pair density index categories ($\chi_3^2 = 1885.975$, $p<10^{-6}$). Eighty-nine percent of the area protected during 2000–2009 was located in landscapes with pair index values greater than 10, and 62% was located in landscapes with pair density index values greater than 60 (Table 1). Contrary to our predictions, in areas with pair density index values greater than 10 (i.e., the bottom 12 rows of Table 1 and Table 2), the distribution of conversion risk differed between protected and unprotected grassland ($\chi_3^2 = 559.102, p<10^{-6}$), and the distribution of cost differed between protected and unprotected grassland ($\chi_3^2 = 17.6022, p = 0.0005$). Broad patterns of differences between protected and unprotected grassland in terms of cost and risk appeared inconsistent, however, with any beneficial targeting scheme. The percent of observed protected grassland in areas with conversion index values of 0 to 25 and 26 to 50 was 9% and 21% (Table 1). The percent of unprotected grassland in areas with conversion index values of 0 to 25 and 26 to 50 was 4% and 11% (Table 2). The percent of observed protected grassland in counties with lower than the median protection cost index of 43 was 63% (Table 1); similarly, 63% of remaining unprotected grassland was in landscapes with protection cost index values below the 50th percentile (Table 2).

Several characteristics of the remaining unprotected grassland in the study area were relevant to our objective of developing ideas for a refined prioritization scheme for easement acquisition and were consistent with our assessment of opportunity for refined targeting. Given recent trends in protection capacity, we focused attention on the 15,938 km^2 of unprotected grassland habitat that was located

in landscapes with pair density index values greater than 23. Most of the grassland habitat in the highest-benefit landscapes was at elevated risk of conversion and was located in counties with below-median protection cost. Eighty percent of the highest-benefit area (12,745 km^2) had a conversion risk index greater than 50 and 72% (11,436 km^2) had a protection cost index below the median. Landscapes with conversion risk greater than 50 and protection cost below the median represented 54% (8,615 km^2) of the total highest-benefit area. Landscapes with conversion risk greater than 75 and protection cost below the median represented 45% (5,710 km^2) of the total highest-benefit area. The intersection of pair density index values greater than 23, conversion risk index values greater than 75, and protection cost below the 25th percentile comprised 25% of the highest-benefit area and encompassed 3,189 km^2 (16th row, 1st column; Table 2).

There were potential improvements in efficiency associated with using a cost-targeted approach to easement acquisition. Observed easement payments exceeded cropland rent in 2009 by a factor of 4.56. Assuming a budget of $10,300,000 and sampling without replacement from the total highest-benefit area until the hypothetical budget was expended led to an overall cost of $442/ha and a protected area of 226 km^2. Sampling from the refined subset of highest-benefit unprotected grassland that was located in landscapes with conversion risk index values greater than 75, and protection cost below the 25th percentile until the budget was expended led to an overall cost of $357/ha and protection of 289 km^2. This was a reduction of 24% in per unit cost and an increase of 20% in area protected.

Discussion

Our assessment indicated that there was need, opportunity, and potential value in integrated targeting of conservation activities in our study area. The need for more integrated targeting of easement acquisition was apparent in our analysis of recent protection activity. Opportunity for refined targeting of protection was revealed in our comparisons of protected and unprotected land: especially the unequivocal evidence of successful targeting of easements to landscapes with higher ecological benefit under the current system. A direction for refining the strategy for future acquisitions was suggested by our analysis of differences in area protected and cost of protection given different targeting criteria.

The amount of habitat protected each year declined steadily during the ten-year period of our study, while per unit easement payments and cropland rental rate increased. Using recently estimated grassland conversion rates and existing unprotected grassland area as a starting point, we projected losses that exceeded or nearly equaled current annual protection. Given recent trends in agricultural land use, it is unlikely that conversion rates will decrease (Carriazo et al. 2009, Stubbs 2007). To offset these trends, the budget for easement acquisition would have to increase in an unprecedented manner. Therefore, targeting of easement acquisition to improve cost efficiency and protect as much of the most at-risk, highest-benefit habitat seemed like an important, and timely, strategic alternative. Maximizing efficiency is an important goal of conservation planning efforts under conditions of increasing loss

rates and land values, and the integration of information about risk of loss and cost of protection can facilitate progress toward this goal (Newburn et al. 2005).

There was clear evidence of successful targeting with a simple, benefits-based approach in our system, and therefore we concluded that there was a clear opportunity to refine current efforts in a simple and straightforward way. The vast majority of the area protected during 2000–2009 was located in targeted, higher-benefit landscapes. Even so, the absence of targeting criteria for conversion risk and land value appeared to have led to protection of less area than would otherwise have been possible. Much of the unprotected intact grassland with the highest predicted waterfowl benefit was nevertheless located in landscape settings where it was expected to be highly vulnerable to conversion or relatively inexpensive to protect. The highest-benefit habitat that was both at highest risk of conversion and lowest cost of protection, however, represented a much smaller proportion of the overall unprotected grassland. Focusing acquisition efforts on this subset of grassland was associated with a potential gain in efficiency of 20% in terms of area protected and 24% in terms of unit cost of protection. Because most of the unprotected grassland was located in landscapes with high levels of conversion risk, the incorporation of information on conversion risk was probably most useful because it helped define an area of 2,042 km^2 with likely lower risk of conversion that could be avoided because of its higher opportunity cost in the context of current protection capacity.

Conservation planners are increasingly recognizing the need for well-informed, integrated approaches to conservation planning with the flexibility to adapt

to change (Newburn et al. 2005, Naidoo et al. 2006, Underwood et al. 2008). In most ecosystems, rates of protection are often low relative to rates of loss and budgets are limited. Grassland ecosystems are likely to face increasing agricultural conversion as world demand for food and energy increases (Hoekstra et al. 2005, Foley et al. 2005). Our assessment of the grassland easement program in the USPPR provided an example of how a refined targeting approach might be developed from relatively simple components and used to increase the effectiveness of current conservation.

Management Implications

Gains in effectiveness are likely to be critical to the future success of conservation efforts in agricultural landscapes like the PPR. Global-scale change in economics, demographics, and climate is predicted to increase worldwide demand for food and energy, while increasing the uncertainty of supply (Ramankutty et al. 2008, Searchinger et al. 2008, Cirera and Masset 2010). As a result, demand for cultivated land is also likely to rise. An adaptive, integrated approach to prioritizing habitat for conservation can help to counter this force by directing conservation activities to areas with a higher benefit-cost ratio. Although we are confident that an integrated targeting scheme would be a useful contribution to conservation efforts in the PPR, we think that continual refinement will be critical to success. Heuristic and rule-based approaches to conservation planning are useful because they are often more likely to be applied (Knight et al. 2008). Furthermore, such approaches can outperform more complex approaches when conservation plans are implemented over multiple years and opportunity for conservation is uncertain (Pressey et al. 1996, Meir

et al. 2004). They are nonetheless useful only to the extent that they accurately represent the system of interest.

Our evaluation was based on a currently applied strategy for assessing ecological value of habitat based on predicted density of breeding duck pairs. The most critical assumption associated with this index is that habitat with higher value for breeding ducks is associated with higher values of pair density. Work is currently underway to assess whether the distribution and abundance of broods of ducks, which might better reflect both pair density and reproductive success, could provide a more complete assessment of habitat value. Regional brood surveys have been ongoing for the past three years and will be used to address this important assumption as enough years of observation are accumulated to provide an accurate representation of the environmental variation that is characteristic of the PPR.

Our assessment indicated that there were 15,938 km^2 in the highest-priority area defined by the current targeting strategy. This area was nearly 6 times larger than the 2,792 km^2 protected during 2000–2009 and was heterogeneous in terms of risk of conversion and cost of protection. We suggest that easement acquisition in the next 10 years could be refocused on the subset of the highest-priority area defined by relatively high risk of conversion and relatively low cost of protection and that gains in efficiency would result. This approach would provide important support to the easement program at a time when its buying power is diminishing, thereby helping to maximize the effect of limited resources, while buying time for efforts to affect land-

use policy in ways that are favorable for grassland conservation (Carriazo et al. 2009).

Economies, policies, and budgets are all dynamic and periods of change provide motivation and opportunity for refocusing of effort. Given recent trends in protection capacity, we think that a structured decision making (Conroy and Peterson 2009) approach to the easement program would be a useful way to identify fundamental objectives, means of achieving those objectives, and critical assumptions. With these components clearly laid out and a refocused strategy, an adaptive approach to ongoing easement acquisition could provide the framework for learning whether fundamental objectives were being attained under the current strategy and for testing key assumptions (Rissman et al. 2007). For example, our proposed approach assumes that integrated targeting will tend to produce a distribution of protected lands with high predicted ecological benefit and relatively high risk of conversion in counties where land values are below the first quartile of land value. This assumption set could be periodically evaluated by comparing the recent easement sample to existing unprotected grassland. More complex monitoring approaches could be used to validate other assumptions. By helping to test key assumptions and incorporate new information in a useful manner, this approach would be most likely to facilitate continued success of the easement program in the changing landscape of the PPR.

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Table 3.1 Area (km^2) of protected grassland by indices of pair density, risk of conversion, and cost of protection. The pair density index was based on the expected density of breeding duck pairs. The conversion risk index was based on the percent area suitable for cultivation. The protection cost index was based on county-level cash rent for cropland.

Protected Grassland						
		Protection Cost				
Pair Density	Conversion Risk	0th-25th	26th-50th	51st-75th	76th-100th	Total
<10	0-25	14	11	9	4	38
	26-50	19	7	19	18	63
	51-75	20	9	59	16	104
	76-100	30	10	54	19	113
10-15	0-25	18	5	7	1	31
	26-50	13	9	19	7	47
	51-75	14	14	34	18	80
	76-100	22	36	42	36	135
16-23	0-25	17	5	10	6	38
	26-50	25	9	17	6	57
	51-75	30	19	51	32	133
	76-100	60	50	83	40	233
>23	0-25	121	27	4	5	157
	26-50	211	135	63	15	424
	51-75	176	111	96	30	413
	76-100	271	173	231	53	728
	Total	1,061	629	797	305	2,792

Table 3.2 Area (km^2) of unprotected grassland by indices of pair density, risk of conversion, and cost of protection. The pair density index was based on the expected density of breeding duck pairs. The conversion risk index was based on the percent area suitable for cultivation. The protection cost index was based on county-level cash rent for cropland.

Unprotected Grassland						
		Protection Cost				
Pair Density	Conversion Risk	0th-25th	26th-50th	51st-75th	76th-100th	Total
<10	0-25	914	535	331	240	2,020
	26-50	1,650	731	466	459	3,307
	51-75	2,229	1,096	978	1,175	5,477
	76-100	3,941	1,879	3,310	4,049	13,178
10-15	0-25	132	85	30	16	262
	26-50	331	198	116	77	722
	51-75	676	538	479	356	2,049
	76-100	1,800	1,381	2,019	1,489	6,689
16-23	0-25	134	45	33	17	229
	26-50	426	236	115	71	847
	51-75	690	498	413	231	1,833
	76-100	1,782	1,504	1,912	1,060	6,258
>23	0-25	581	169	70	14	833
	26-50	1,461	610	228	60	2,360
	51-75	1,806	1,098	655	143	3,702
	76-100	3,189	2,522	2,607	725	9,043
	Total	21,744	13,123	13,762	10,182	58,811

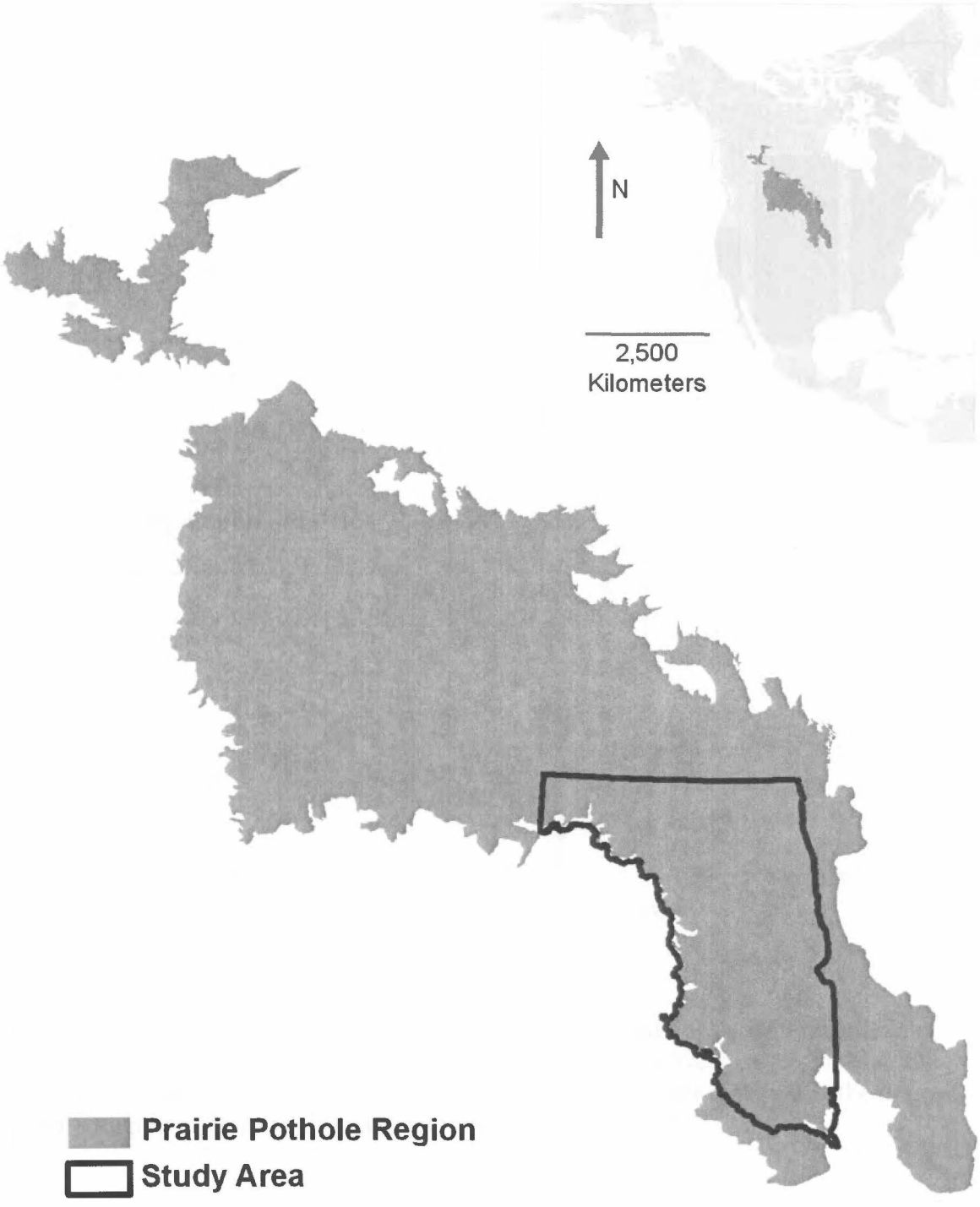

Figure 3.1 Location and extent of the study area (Prairie Pothole Region of North and South Dakota) within North America and the Prairie Pothole Region.

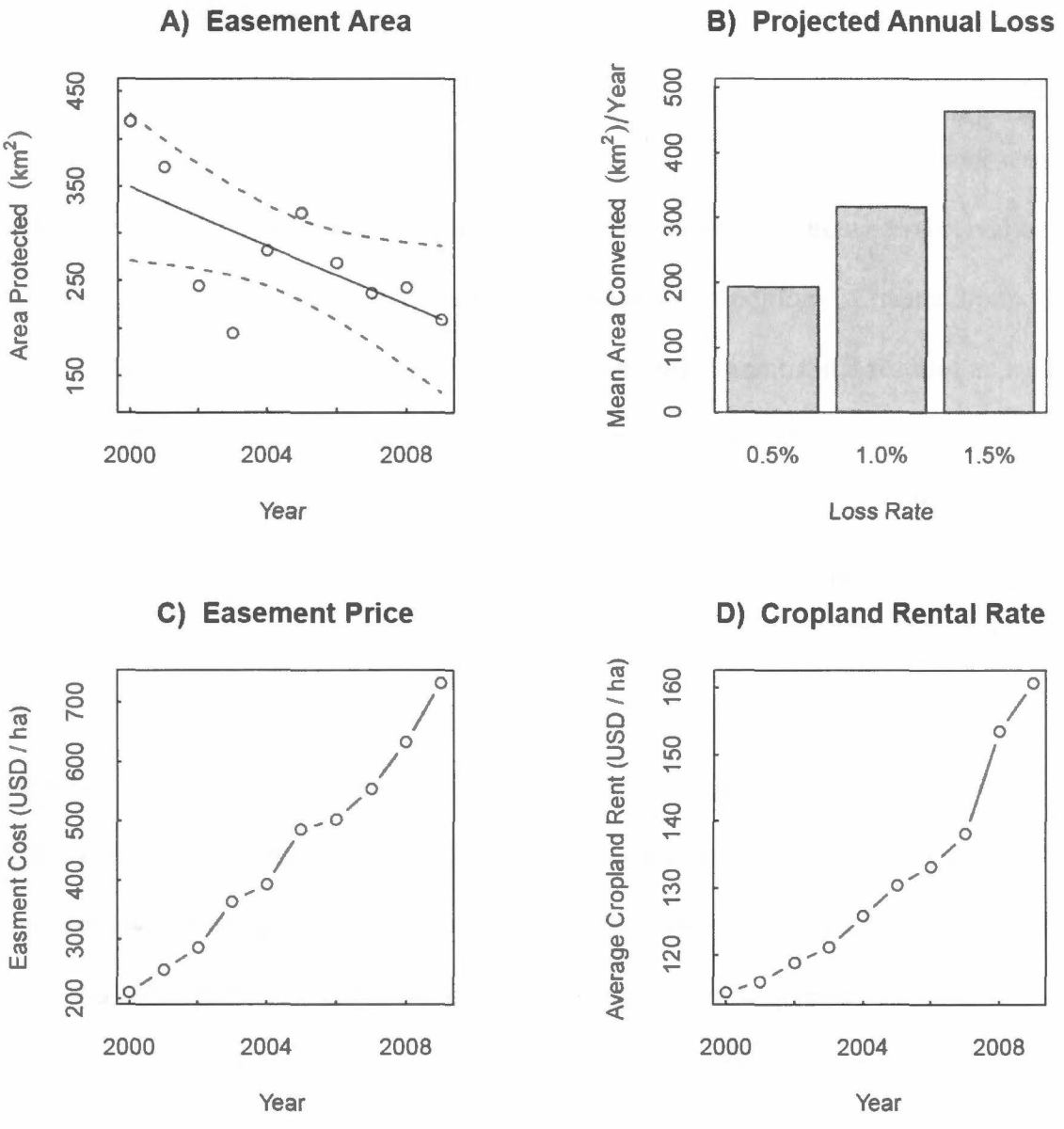

Figure 3.2 A) Trend in recent easement acquisition (dashed lines are 95% confidence limits for the solid regression line), B) projected grassland conversion to cropland, C) observed easement cost, and D) average reported rental rates for cropland in the Prairie Pothole Region of North and South Dakota during 2000–2009.

GENERAL CONCLUSIONS

My work was focused on parameters and conservation activities that are thought to influence reproductive success of ducks in the PPR. The objective of this work was achieved. Chapter 1 provided new knowledge about relationships between survival of duck nests and spatiotemporal variation in environmental conditions. Chapter 2 provided new knowledge of relationships between brood distribution and habitat features as well as evidence of the feasibility of an extensive brood survey in the PPR. Chapter 3 suggested a path toward more informed targeting of easement acquisition that could ultimately result in a more efficient process for prioritizing conservation activities in the PPR.

The 8-year, 52-site study relating nest survival of ducks to spatiotemporal variation in environmental conditions was one of the most extensive studies of this important demographic rate ever conducted in the highly variable environment of the PPR. This effort resulted in a data set comprising nest histories for 12,754 nests of the most common duck species in the region. The combination of contemporary statistical modeling techniques and recent GIS data describing landscape-level environmental variation among sites and years revealed patterns in these data that were consistent with most predictions but inconsistent with others. Consistent with predictions, nest survival probability was highly variable among sites and years. Estimates of average site-level nest survival probability ranged nearly 12-fold from 0.02 ($\widehat{SE}$ = 0.01) to 0.23 ($\widehat{SE}$ = 0.02). Surprisingly, nest survival probability was only weakly related to relatively static environmental variables like the proportion of perennial cover in the landscape surrounding the study site. These variables have been important in several past studies of

nest survival (Greenwood et al. 1995, Reynolds et al. 2001, Stephens et al. 2005), but were not strong predictors of nest survival in my study.

Nest survival was much more strongly related to current and recent levels of spatiotemporally dynamic environmental variables: including spring pond density and gross primary productivity. These relationships were complex and provided support for the general hypothesis that periodic pulses of productivity measured over short time scales of 1-2 years had the potential to affect nest survival of ducks in the PPR. These effects, moreover, were likely indirect because most nest failures result from nest destruction by mid-sized, generalist, mammalian predators (Sargeant et al. 1993). Nest survival was positively related to spring pond density and primary productivity in the current year. Nest survival was negatively related to spring pond density two years before and to primary productivity in both the previous year and two years before (Chapter 1). This 'memory' of past conditions was a novel result and was relevant to ideas about population dynamics that might result from combined spatial and temporal variation in environmental conditions. Lagged effects of environmental conditions on population dynamics have been observed in other systems for a variety of taxa, but we observed these patterns at a smaller temporal scale than usually observed in broad-scale studies of climate effects and marine systems (Owen-Smith et al. 2005, Sandvik et al. 2005, Stenseth et al. 2003). Furthermore, the clear signal in the data, i.e., that the highest nest survival probability would be associated with the initial year of high pond density and primary productivity following two or more years of low pond density and primary

productivity, was consistent with the idea that the PPR ecosystem was being broadly affected by periodic variation in precipitation.

Pulse-reserve responses are a characteristic of ecosystems where pulses of resources enter the system and create a spike in productivity that resonates throughout the ecosystem and then dampens through time until the next pulse (Schmidt and Ostfeld 2008). An unique feature of the PPR is its millions of glacially-formed wetland basins that might provide reservoirs of productivity that could amplify the effects of resource pulses. The observational study design that I used was necessitated by an interest in *in situ* environmental conditions and could not lead to definitive conclusions about causation. However, my results were consistent with the idea that pulses of resources were affecting both predators and prey in my study system (Holt 2008). Much of the past research on duck populations in the PPR has focused on the direct effect of predators on reproductive success (Greenwood et al. 1995, Reynolds et al. 2001, Pieron and Rohwer 2010) and endogenous limitation through density dependence (Viljugrein et al. 2005, Sæther et al. 2008). Placing future investigations in the broadened context suggested by my results could help to resolve some of the uncertainty about the roles of individual quality, endogenous processes like density-dependence, and environmental conditions in population dynamics in the variable environment of the PPR.

The results of my investigation of nest survival had two major implications for management of duck populations. Habitat management for ducks in the PPR has been based on spatial and temporal patterns of the distribution and abundance of breeding pairs and relationships of reproductive success to habitat characteristics (United States Fish

and Wildlife Service and Canadian Wildlife Service 1986, Johnson et al. 1994). The observations from my study indicated that nest survival was more strongly related to spatiotemporal sources of environmental variation. This suggests that quality habitat for breeding ducks is probably 1) difficult to identify without including information about pond density and primary productivity in current and recent years and 2) is characterized in part by cycles of natural variability in precipitation. Efforts to conserve quality habitat for breeding ducks that are informed by knowledge of landscape-level responses to cycles of precipitation are therefore likely to be more effective. Combined spatial and temporal variation in primary productivity and wetland conditions appears to potentially affect reproductive success of ducks as much or more than spatial variation in landcover or wetland density, thus there is a need to better understand the resonant frequencies and temporal cycles of productivity and wetness in the PPR in order to make informed conservation and management decisions in the face of large-scale environmental change.

The extensive brood survey that I analyzed and interpreted in Chapter 2 successfully provided an informative and geographically extensive picture of the distribution of broods in late summer. To my knowledge this study was the most extensive study of unmarked duck broods in the PPR attempted to date. It was also the only study that related probability of occupancy to landscape-level habitat covariates. The advancements represented by this study were made possible by recent progress in the theory and application of hierarchical statistical models for count survey data (Royle and Dorazio 2008). Using a repeat-visit survey design based on three surveys of a wetland basin in a 24-hour period and hierarchical mixed-effects models for presence-non-

detection data, I was able to 1) simultaneously model both probability of occupancy and probability of detection relative to covariates, 2) select among competing models of detection probability and probability of occupancy, and 3) simultaneously estimate the probability that a wetland basin was occupied by a brood and the probability that a brood was detected given that a brood was present. I estimated probability of occupancy and probability of detection for each of the five most common species of ducks in the study area, and I tested predictions about relationships of these probabilities to covariates.

The brood survey successfully provided information about brood occupancy of wetlands over a large spatial extent. Detection histories comprising 13,068 surveys of 3,226 wetland basins on 167 study sites over three seasons provided ample data for modeling. Models performed well for all five species. They provided reasonable approximations of structural parameters and displayed no evidence of lack-of-fit. I therefore concluded that this sampling design and analysis approach was a useful combination for evaluating occupancy of wetlands by broods across the study area.

I observed relationships between brood occupancy at the scale of both wetland basins and landscapes. Consistent with predictions based on previous studies of nest survival and density of breeding pairs, I observed that probability of occupancy increased with wetland size for all five species and increased with the proportion of perennial cover in the landscape for all species except mallard (*A. platyrhynchos*). Estimated median probability of occupancy (lower 90% Credible Interval, upper 90% Credible interval) by a gadwall (*A. strepera*) brood increased from 0.08 (0.07, 0.10) to 0.28 (0.24, 0.33) as wetland area increased from 0.19ha to 2.12ha. Estimated probability of wetland

occupancy by a gadwall brood increased from 0.12 (0.09, 0.16) to 0.20 (0.16, 0.25), as the proportion of perennial grass cover on the 10.4-km^2 study site increased from 0.03 to 0.99.

Median probability of detection was low (generally <0.30) and variable. I concluded that this parameter must be dealt with directly during the design and analysis of brood surveys (Pagano and Arnold 2009). Broods were detected on only 3% to 12% of wetland basins, but species-level estimates of probability of occupancy indicated that from 9% to 35% of basins were occupied.

Extensive brood surveys represent a useful tool for identification of landscapes and wetland basins that are associated with consistently higher probability of occupancy by broods. Reliable, model-based estimates of probability of occupancy at the patch scale can be used to identify conservation priorities at larger scales (Gardner et al. 2010). For example, the subpopulation of wetlands that tends to be occupied by broods in a higher proportion of years could be a higher conservation priority. The subpopulation of landscapes of a given size that is associated with a higher proportion of occupied wetlands could also be prioritized. Given the success of the initial effort (Chapter 2), it is likely that the brood survey will be continued in future years and be used along with breeding pair surveys to guide management.

Knowledge of ecological relationships and habitat value is likely not enough to accomplish conservation goals given current threats to wildlife habitat (Pressey et al. 2007). Targeting limited funds for habitat conservation as effectively as possible has become a more important concern given limited budgets, ongoing habitat loss, and

uncertainty about large-scale drivers of land-use such as demand for food and fuel (Foley et al. 2005, Ramankutty et al. 2008). I evaluated the need and opportunity for refined targeting of habitat protection efforts for breeding ducks given recent trends in land prices and protection capacity. I used available information from the United States Fish and Wildlife Service (USFWS) and the United States Department of Agriculture (USDA) to assess recent trends in acquisition of permanent conservation easements acquired by USFWS for migratory bird habitat (Chapter 3). The USFWS easements permanently prohibit cultivation of grassland and wetland habitat and thus would provide the greatest conservation value when targeted to landscapes where valuable habitat for migratory birds is at high risk of conversion and can be protected for a relatively low cost. Grassland easements are currently targeted based on an index to density of breeding duck pairs. I investigated whether there was a need for refined targeting by examining 1) recent (2000–2009) trends in area protected, 2) projected losses of habitat, 3) recent unit costs of protection, and 4) recent rental rates for cultivated land across the study area. I investigated whether there was opportunity to refine current targeting by comparing the distribution of recently protected land and unprotected land in terms of pair density, risk of conversion to cropland, and likely cost of protection. I developed indices of conversion risk based on Land Capability Class, which is an index of suitability for cultivation that is related to the probability of conversion (Stephens et al. 2008, Rashford et al. 2010). I developed an index of protection cost based on the average county-level cropland rental rate which is related to land value (Xu et al. 1993, Naidoo et al. 2006)

There was a clear need for refined targeting of habitat protection in the PPR. The area of habitat protected declined each year during (2000–2009). Estimated area protected in 2000 was 349 km^2 (95% Confidence Interval: 272 km^2 to 425 km^2) and in 2009 was 210 km^2 (133 km^2 to 287 km^2). Cropland rental rates concurrently increased 40% and cost of protection concurrently increased 248% from $210/ha to $730/ha and.

I also identified a clear opportunity for refined targeting through comparison of the protected and unprotected grassland. There was evidence that the currently used straightforward targeting system based on a categorized index of pair density had concentrated 89% of the protected area in the highest-priority areas. The remaining unprotected grassland area of highest conservation priority based on pair density was nearly 6 times larger than the 2,792 km^2 protected during 2000–2009. Categorizing this area based on conversion risk and protection cost defined a much smaller area of about 3,189 km^2 that was located in landscapes of highest priority based on pair density and was also composed of land that was 75% potential cropland and was located in counties that had average cropland rental rates below the 25th percentile. Sampling randomly from these two populations of unprotected areas indicated a 24% potential difference in per/hectare cost of protection and a 20% potential difference in area protected.

I concluded that refocusing easement acquisition efforts on the smaller area defined by higher conversion risk and lower potential cost of protection was a logical way to increase the efficiency of easement acquisition activity. I suggested that this strategy be implemented as part of a larger structured decision making exercise that would give rise to an adaptive strategy for monitoring progress and evaluating

assumptions. To my knowledge, this study was the first attempt to increase conservation effectiveness in this important region for migratory birds by reprioritizing protection efforts based on combining information about ecological benefits, risk of conversion, and cost of protection.

Ecology, wildlife management, and conservation planning are complimentary and intertwined disciplines. Rigorously derived scientific knowledge of basic ecology provides a solid foundation for management and conservation planning, and science-based wildlife management and conservation planning helps to ensure that ecosystems like the PPR can continue to provide large populations of migratory birds with critical breeding habitat. Strong curiosity about birds and a deep interest in conservation provided much of my personal motivation to work on the studies in my dissertation. These studies were built on a rich foundation of past work and took advantage of developments in sampling and analysis to contribute new knowledge. I hope they will in turn provide part of the substrate for future developments.

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